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COVER: Wilson's Phalaropes (*Phalaropus tricolor*). Illustration by Robin Corcoran.

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FRONTISPIECE. Painting of three Mexican *Arremon* brush-finches, including *A. brunneinucha brunneinucha* (top; MZFC 4462, Mexico, Veracruz, Monte Blanco, 5 km E Teocelo), *A. kuehnerii* (middle; MZFC 3986, Mexico, Guerrero, El Iris, Tlacotepec), and *A. virenticeps* (bottom; MZFC 21462, Mexico, Jalisco, Municipio San Sebastián del Oeste, carretera San Sebastián a la Bufa)

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A NEW SPECIES OF BRUSH-FINCH (*ARREMON*; EMBERIZIDAE) FROM WESTERN MEXICO

ADOLFO G. NAVARRO-SIGÜENZA,[1]
MARTHA A. GARCÍA-HERNÁNDEZ,[1] AND A. TOWNSEND PETERSON[2,3]

ABSTRACT.—A new highland species of chestnut-capped *Arremon* brush-finch is described from the Sierra Madre del Sur of central Guerrero. This form, although indistinguishable in external phenotype from adjacent populations to the east in Oaxaca, is dramatically differentiated in mitochondrial DNA sequence characters, and quite unexpectedly is the sister lineage to the very distinct (phenotype and genotype), central-Mexican-endemic *A. virenticeps*. Nuclear sequence differentiation in the new lineage is more subtle than in mitochondrial DNA, but is on par with that in the well-marked *A. virenticeps*. The new species is thus distinct from its sister lineage in genotype and phenotype, and clearly distinct from all other forms in genotype; however, it has retained an ancestral external phenotype similar to other members of the broader *A. brunneinucha* complex. *Received 9 August 2012. Accepted 11 February 2013.*

Key words: cloud forest, cryptic species, Mesoamerica, new species, species complex, species limits.

The *Arremon brunneinucha* brush-finches of montane cloud forests of the Neotropics have long been recognized as a difficult complex, showing dramatic patterns of population differentiation (Chapman 1923; Moore 1938; Parkes 1954, 1957, 1959; Paynter 1978; Remsen and Graves 1995). The group, formerly considered a separate genus, *Buarremon*, has traditionally been classified into three species: *A. virenticeps* of central Mexico, *A. torquatus* of northern South America, and the highly polytypic and broadly distributed *B. brunneinucha* (Dickinson 2003). Detailed molecular studies indicated polyphyly of this group with respect to distinct lineages of *Arremon* and the related genus *Lysurus* (Flórez-Rodríguez et al. 2010), leading authorities recently to submerge several genera into *Arremon* (Remsen et al. 2012).

Early molecular studies indicated considerable population structuring in this group, with allozyme-based analyses showing high degrees of differentiation among populations of *A. brunneinucha* just within Mexico (Peterson et al. 1992). Subsequent, sequence-based analyses (Cadena et al. 2007, Navarro-Sigüenza et al. 2008) also found strong differentiation among populations, and demonstrated that *A. torquatus* is not closely related to the other two species; one study (Cadena et al. 2007) indicated that *Buarremon* is not monophyletic (see also Flórez-Rodríguez et al. 2010). These studies also revealed that *A.*

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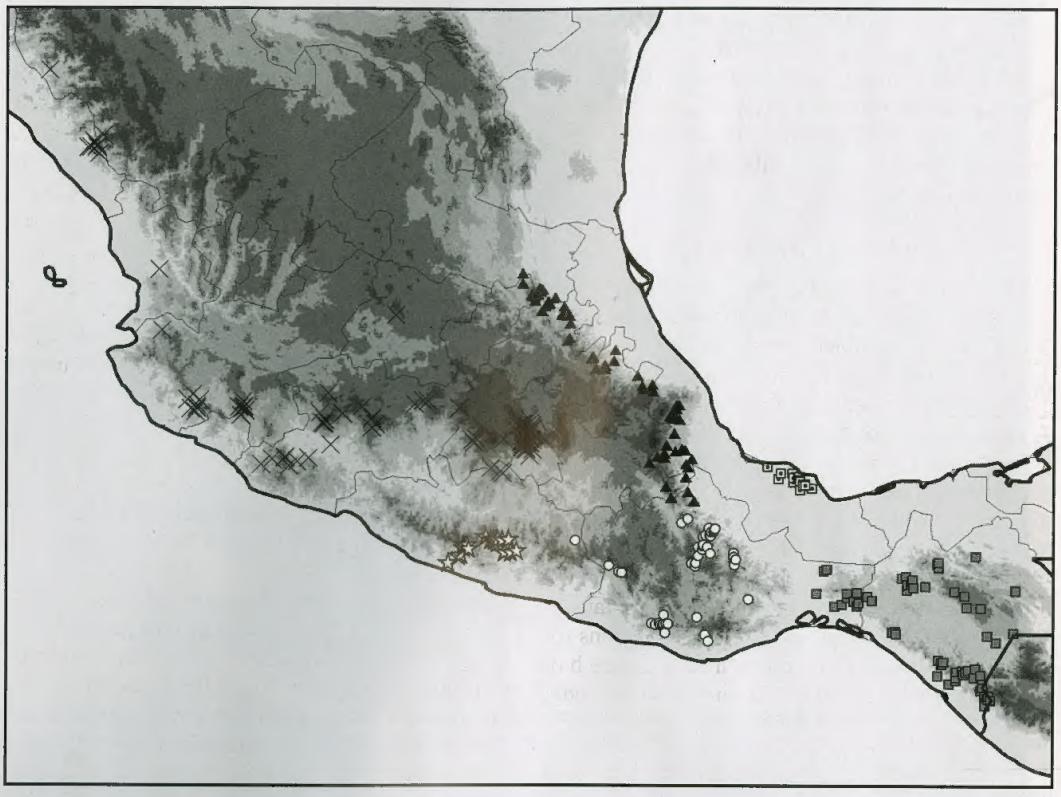

FIG. 1. Map of central Mexico, showing the known distribution of relevant *Arremon* forms in Mexico: dotted squares = *A. brunneinucha apertus*, black triangles = *A. b. brunneinucha*, white circles = *A. b. suttoni*, gray squares = *A. b. macrourus*, X's = *A. virenticeps*, stars = *A. kuehnerii*. Different shades of gray indicate elevational intervals of 500 m.

virenticeps was derived from within *A. brunneinucha*, leaving the latter paraphyletic. As *A. torquatus* and *A. virenticeps* both have striped crowns and are so similar as to have been considered conspecific by many authors (e.g., Paynter 1970), these results underline the complex evolutionary patterns in phenotype and genotype in this group.

The chestnut-crowned populations in the highlands of Guerrero (Fig. 1) have traditionally been allocated to the subspecies *A. brunneinucha suttoni* of central and western Oaxaca, and yet differ from those populations markedly in mitochondrial DNA sequences (Navarro-Sigüenza et al. 2008). Indeed, phylogenetic reconstructions (Navarro-Sigüenza et al. 2008) indicated that the sister lineage to the populations from Guerrero is the geographically adjacent (to the north) but very distinct *A. virenticeps*, rather than the chestnut-crowned populations to the east (Oaxaca), and that the populations from Guerrero differ in mitochondrial DNA sequence composition from all other samples in the study by ≥26 of 800 base pairs evaluated (including at least one transversion in each pairwise comparison). In spite of this dramatic genetic differentiation, this lineage has retained an ancestral phenotype, and therefore is not visibly distinct from chestnut-crowned populations in Oaxaca (see Frontispiece).

Given the above evidence, the chestnut-capped *Arremon* populations of central Guerrero represent a taxon and evolutionary lineage separate from Oaxaca populations (*A. brunneinucha suttoni*) with which they have been synonymized. The type locality of *A. b. suttoni* is La Cumbre, 5 miles northeast of Cerro San Felipe, in northern Oaxaca, Mexico, far from the populations of Guerrero; indeed, no names that have been applied to Mexican *Buarremon* come from sites within or near to Guerrero, such that no name is available for the populations from Guerrero. In this contribution, we expand on the findings of the

mitochondrial DNA studies via examination of four nuclear genes, and find that the populations from Guerrero are dramatically distinct from the lineages that are most closely related to them; because no existing name is available from Guerrero, we herein describe the taxon as *A. kuehnerii*, sp. nov.

MATERIALS AND METHODS

This study is based partly on our previous phylogeographic studies (Navarro-Sigüenza et al. 2008), where complete methods and sampling details are provided for mitochondrial DNA sequencing. Our mitochondrial sequences spanned the 3′ end of the cytochrome oxidase subunit II gene (26 bp), the complete tRNA-lysine (70 bp), the complete ATPase subunit eight gene (168 bp), and the 5′ end of the ATPase subunit six gene (537 bp; Navarro-Sigüenza et al. 2008; for simplicity, we call this mitochondrial fragment ATP8).

Here, we supplement the mitochondrial data by sequencing the following nuclear gene regions for 14 individuals including representatives of each of the major clades identified in our previous study: the fifth intron of the β-fibrinogen gene (Fib5), the eleventh intron of the glyceraldehyde-3-phosphodehydrogenase gene (G3PDH), the third intron of the lactate dehydrogenase gene (LDH), and the fifth intron of the transforming growth factor β2 gene (TGF). Sequencing protocols for the nuclear markers followed Moyle et al. (2012) and Sangster et al. (2010). We inferred haplotype phases of heterozygous individuals with the coalescent-based Bayesian method PHASE 2.1 (Stephens and Donelly 2003), as implemented in DNAsp 5.0 (Librado and Rozas 2009). Haplotype networks were generated using the program TCS ver. 1.21 (Clement et al. 2000).

We performed Bayesian estimation of tree topology on the concatenated dataset of mitochondrial and nuclear sequences using MrBayes 3.2.1 (Ronquist et al. 2012). Markov chains were run for 10^7 generations, sampling every 2,000 generations, using two concurrent runs and three heated chains for each cold chain. The substitution matrix, base frequencies, and gamma shape parameter were unlinked between data partitions, and the rate prior was set to variable, allowing partitions to evolve at different rates. The dataset was partitioned by gene, and MrModeltest 2.3 (Nylander 2004) was used to select the appropriate model of sequence evolution under the Akaike Information Criterion (AIC) for each data partition. Tracer 1.5 (Rambaut and Drummond 2007) and the parameter statistics output of MrBayes 3.2.1 were used to examine convergence of parameter estimates and determine appropriate burn-in runs; Are We There Yet? (AWTY; Wilgenbusch et al. 2004) was used to assess the convergence of clade posterior probabilities.

For phenotypic comparisons, we measured individuals of large series of modern specimens of both sexes from the new taxon ($N = 65$), *A. b. suttoni* ($N = 63$), and *A. b. brunneinucha* ($N = 46$), from the collections of the Museo de Zoología of the Facultad de Ciencias, and the Instituto de Biología, both at the Universidad Nacional Autónoma de México. On each specimen, we measured bill length (anterior edge of nostril to tip), bill depth (at anterior edge of nostril), tarsus length (to lowest undivided scute), wing chord, and tail length (from base of central rectrices to tip of longest rectrix). We measured each individual for each measurement three times, and averaged the three values. We calculated medians and ranges for each variable in each population and sex, and inspected distributions visually for differentiation of the populations from Guerrero. We conducted a discriminant function analysis in R (R Core Development Team 2008), and derived overall statistical significance and correct classification efficiency values as reflections of overall degree of morphometric differentiation. We also made detailed comparisons of coloration and plumage patterns among these series, with color terminology based on Smithe (1975).

Arremon kuehnerii, sp. nov. (Fig. 2)

Holotype.—Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City, Mexico, MZFC 18084, adult male, from Carrizal de Bravo (17.60° N, 99.83° W; elevation 2,400 m), Municipio Fernando Bravo, Guerrero, Mexico; Markus Mika, collector, 12 January 2004. GenBank accession numbers EU364933, KC665981, KC665993, KC666006, and KC666018.

Paratypes.—MZFC 8515, adult female; MZFC 8516, adult male; and MZFC 8517, adult unsexed; all from El Iris (17.48° N, 100.20° W; elevation 2,200 m), Municipio Heliodoro Castillo, Guerrero, Mexico; Adolfo G. Navarro-Sigüenza, collector, 17 June 1989.

Other Material Examined.—Arremon virenticeps: MZFC 5655-8, 5660-3, IBUNAM 26943. *A. kuehnerii*: MZFC 1467, 3976-80, 3984-7, 3989,

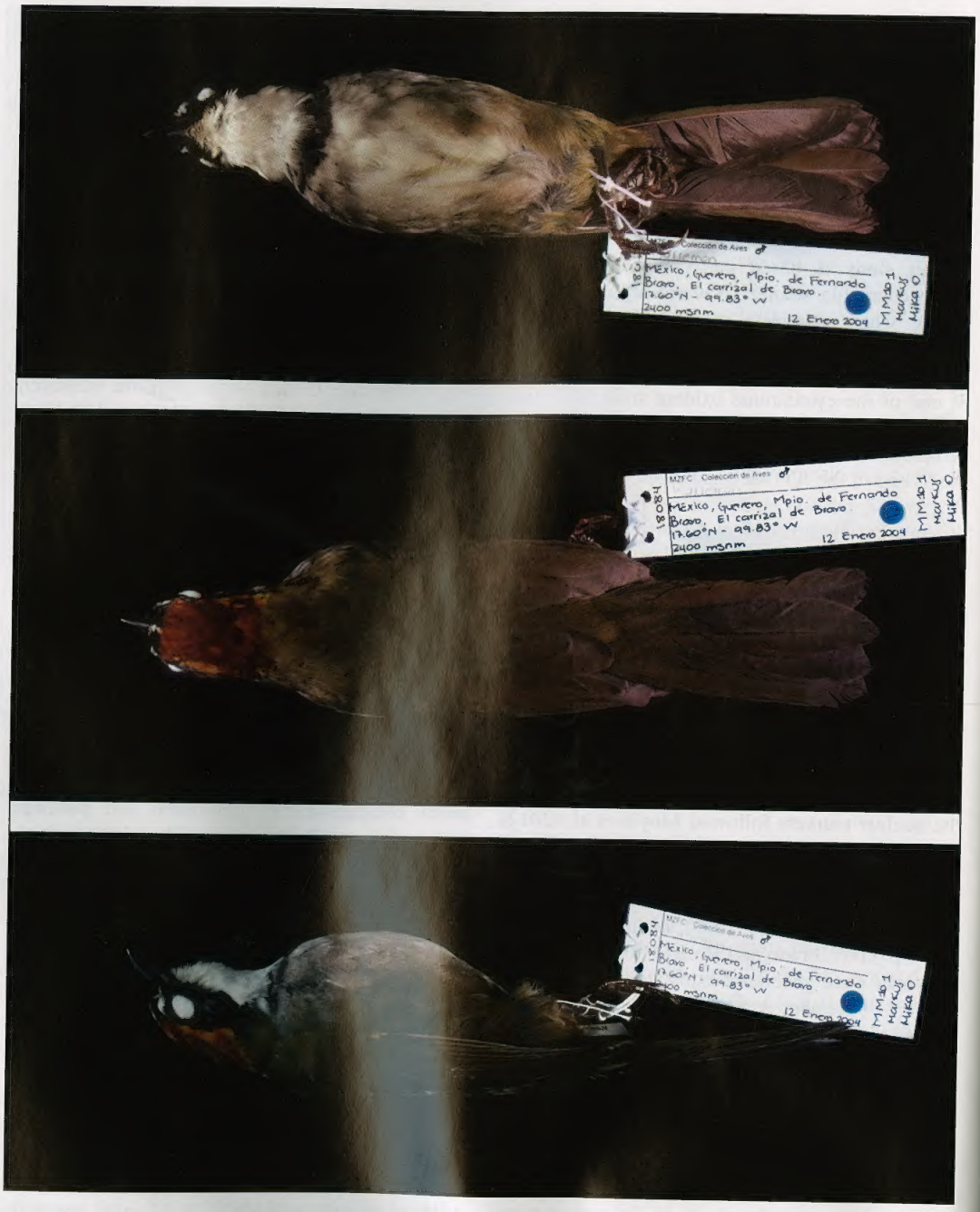
MZFC Colección de Aves
México, Guerrero, Mpio. de Fernando Bravo, El carrizal de Bravo.
17.60°N - 99.83° W
2400 msnm
12 Enero 2004
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FIG. 2. Photographs of the holotype of *A. kuehnerii* (MZFC 18084) from ventral, dorsal, and lateral views.

4808-12, 7526-7, 7552, 7556-8, 8510-7, 17554, 17761, 18084-5, 18227-8, 19328, 21401, 22152; IBUNAM 10575-91, 16213, 20508, 20886, 22045-6, 22838. *A. "b." brunneinucha*: MZFC 8470, 8475-7, 8500-1, 9395-6, 9404, 9606, 9489, 9510, 9520, 9880-1, 9893-4, 9885, 9916, 10356-7, 10389, 10636, 11325-7, 11494, 15209-11, 19305-12, 22021-3; IBUNAM 16214, 16258, 16218, 16221,

16226. *A. "b." suttoni*: MZFC 7608, 7637-8, 7641, 7650, 7656, 7658, 8076-8, 8385, 8584, 9784, 10089, 11255, 11257-61, 11263, 11265-7, 12351, 12262, 12707, 12713, 12717, 12729, 12746, 12782, 12786, 12813, 12822, 12866, 12968, 16673-4, 17996, 17999, 21966, 21969-70, 23098-9; IBUNAM 10592-5, 16215, 16217, 16219-20, 16223-4, 16228-30, 22047-9, 22755, 28101. In broader comparisons, we examined all *Arremon* holdings of the Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México; Field Museum of Natural History; University of Kansas Biodiversity Institute; and Museum of Vertebrate Zoology. From information in the *Atlas of Mexican Bird Distributions* (Navarro-Sigüenza et al. 2003), additional specimens of *A. kuehnerii* are held at the American Museum of Natural History (1), Bell Museum of Natural History (1), Natural History Museum (Tring; 6), California Academy of Sciences (28), Canadian Museum of Nature (7), Delaware Natural History Museum (6), Field Museum of Natural History (2), Instituto de Historia Natural (1), Los Angeles County Museum of Natural History (1), Louisiana State University Museum of Natural Science (2), Moore Laboratory of Zoology (50), Museum of Comparative Zoology (10), Texas Cooperative Wildlife Collections (1), and U.S. National Museum of Natural History (4).

Morphological Diagnosis.—A medium-sized emberizid finch with chestnut crown, ochre supercilium, black mask, and green-olive back; white throat separated from white-and-gray belly by black, crescent-shaped collar. *Arremon kuehnerii* is not distinguishable from *A. b. suttoni* and other members of the *A. b. brunneinucha* complex in terms of mensural characters or plumage coloration.

Molecular Diagnosis.—The six samples of *Arremon kuehnerii* included in the molecular study were sequenced previously for an 800-bp segment of the mitochondrial genome (Navarro-Sigüenza et al. 2008). Within this segment, *A. kuehnerii* showed unambiguously eight diagnostic bases: T at base 78 and T at base 147 of ATPase8, and G at base 72, T at base 117, C at base 183, T at base 342, G at base 414, G at base 427 of ATPase6, as compared with series totaling 73 highland *Arremon* brush-finches, including representatives of populations from all major humid-montane forest patches in northern Mesoamerica (Navarro-Sigüenza et al. 2008; all base designations refer to the sequence for the holotype, deposited in GenBank as EU364933).

The nuclear sequence dataset covered 14 individuals, with a total alignment length of 2,122 bp of combined DNA sequences from four genes: Fib5 (579 bp), G3PDH (361 bp), LDH (608 bp), and TGF5 (574 bp). New sequences generated for this study were deposited in GenBank (accession numbers KC665971-KC666021). Models of sequence evolution used for Bayesian analysis of combined mitochondrial and nuclear sequence data were: GTR + I for ATP8; HKY for G3PDH; HKY + I for TGF5; and F81 for Fib5 and LDH.

Analyses of the concatenated data set indicated convincingly that the sister lineage to the populations from Guerrero are the stripe-headed finches referred to as *Arremon virenticeps*—support for this sister relationship was strong in all analyses (Fig. 3A). Haplotype networks for the five genes studied showed varying degrees of differentiation among populations (Fig. 3B–F). ATP8 showed strong differentiation, with subsets of the networks being effectively unlinked among most of the forms. The nuclear genes showed greater mixing, although tendency toward sorting was noted in G3PDH and Fib5; we note that the species *A. virenticeps* is similarly incompletely sorted with respect to other populations in the complex. The populations from Guerrero were clearly differentiable from their sister lineage *A. virenticeps* based on numerous sequence characters from multiple genes.

Description of Holotype.—Crown chestnut, eyebrow yellow-ochre, lores and small forehead stripe white within black mask extending from side of neck across face; bill black. Nape, back, rump, and upper surface of rectrices light olive-green, somewhat deeper on tail. Throat white. Crescent-shaped black band across chest, below which belly is white bordered laterally by medium gray with some intermixture of light olive. Undertail coverts and underside of rectrices sandy olive-green. Legs very dark brown on dried skin.

Description of Paratypes.—The paratypes are closely similar to the holotype in external phenotype, and only minor phenotypic variation exists across the type series.

Measurements (in mm).—Holotype, with variation in entire series examined shown in parentheses as ranges; measurements in mm. Bill length 10.9 (males 8.5–14.4, females 10.5–13.8), bill depth 7.4 (males 6.3–8.8, females 6.2–8.5), wing length 86 (males 76.6–85.8, females 77.6–84.2), tail length 88 (males 83.2–96.6, females 82.3–88.3), and tarsus length 28.6 (males 26.4–28.3, females 26.1–27.5).

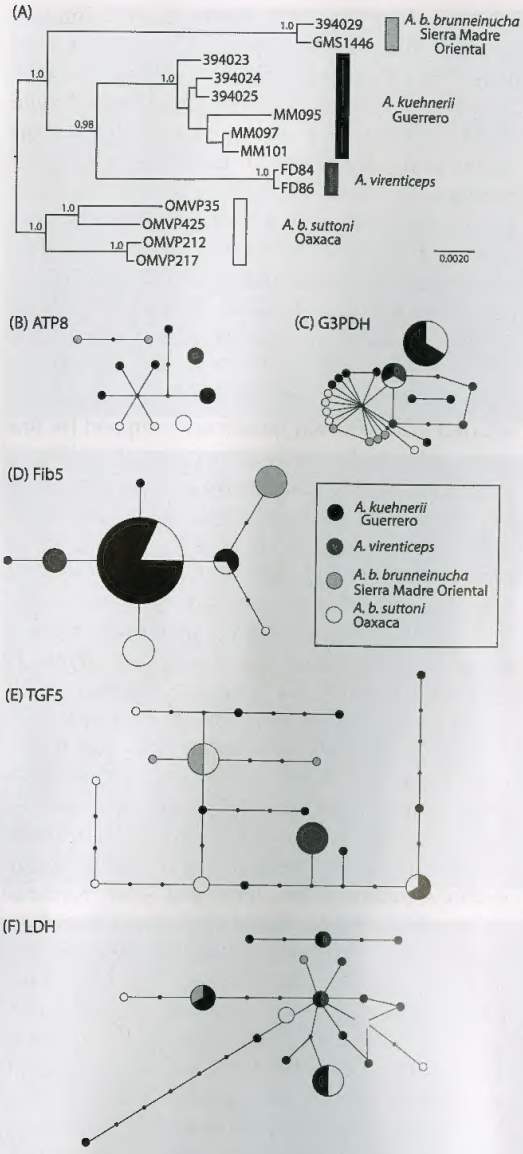

FIG. 3. (A) Bayesian majority-rule consensus tree of relationships among relevant *Arremon* brush-finches inferred from the concatenated mitochondrial and nuclear dataset of five genes. Numbers above branches indicate Bayesian posterior probabilities above 0.95. Tips refer to collection numbers for specimens as in Navarro-Sigüenza et al. (2008). Haplotype networks for each gene are shown in (B), (C), (D), (E), and (F). Disconnected haplotypes are >6 steps away from their nearest haplotypes. Circle diameters are proportional to numbers of individuals sharing a haplotype. Black shaded areas, *Arremon kuehnerii*; light gray, *A. b. brunneinucha*; dark gray, *A. virenticeps*; and clear, *A. b. suttoni*.

Etymology.—The new species is named for Carl Kuehner, in honor of his long-standing engagement and dedication to fish and wildlife management in the United States and more broadly across the Americas. He has devoted significant time and effort to supporting conservation efforts by many organizations, including the National Fish and Wildlife Foundation. Mr. Kuehner leaves a significant legacy to the conservation and management of the world's natural resources.

Ecological and Distributional Notes.—All members of the *Arremon brunneinucha* (*sensu lato*) complex are associated with cloud forest or humid pine-oak forest. The distribution of the complex reflects this connection: in Mexico, its representatives are found on each of the major mountain masses (Fig. 1). The broader distribution of the complex is coextensive with that of cloud forest in the Americas, save for lack of representation in the tepui and Atlantic forest regions of South America. Although *A. virenticeps* ranges into adjacent habitat types (e.g., dry pine-oak forest, fir forest), it is clear that the clade is generally associated tightly with cloud forest and other humid montane forest types. *A. kuehnerii* is common in humid montane forest in central Guerrero, and is likely not under any immediate conservation threat; in the longer term, the species could be threatened by continued habitat destruction in the region.

Comparisons.—*Arremon kuehnerii* is closely similar in all phenotypic respects to *A. b. suttoni*, and in fact we perceive no means of distinguishing it, save for molecular analyses or consideration of geographic range (see Frontispiece; vocal characteristics are presently poorly known, but are not markedly differentiated). Compared with *A. b. brunneinucha* of northeastern Mexico, *A. kuehnerii* has more white and less slate gray on the breast and belly but is otherwise similar. *A. b. apertus* of the Tuxtlas Massif of southeastern Mexico lacks the black chest band present in all other Mexican chestnut-capped *Arremon* forms (Paynter 1978). Most relevant, *A. kuehnerii* is clearly and easily distinguishable from its sister lineage (*A. virenticeps*) based on its solid chestnut crown, as compared with the striped crown in *A. virenticeps*.

Mensural data indicate that *Arremon kuehnerii* is closely similar to other Mexican species. Indeed, in every dimension measured, the range of measurements of individuals of the new form overlaps with the ranges for *A. b. suttoni* and *A. b.*

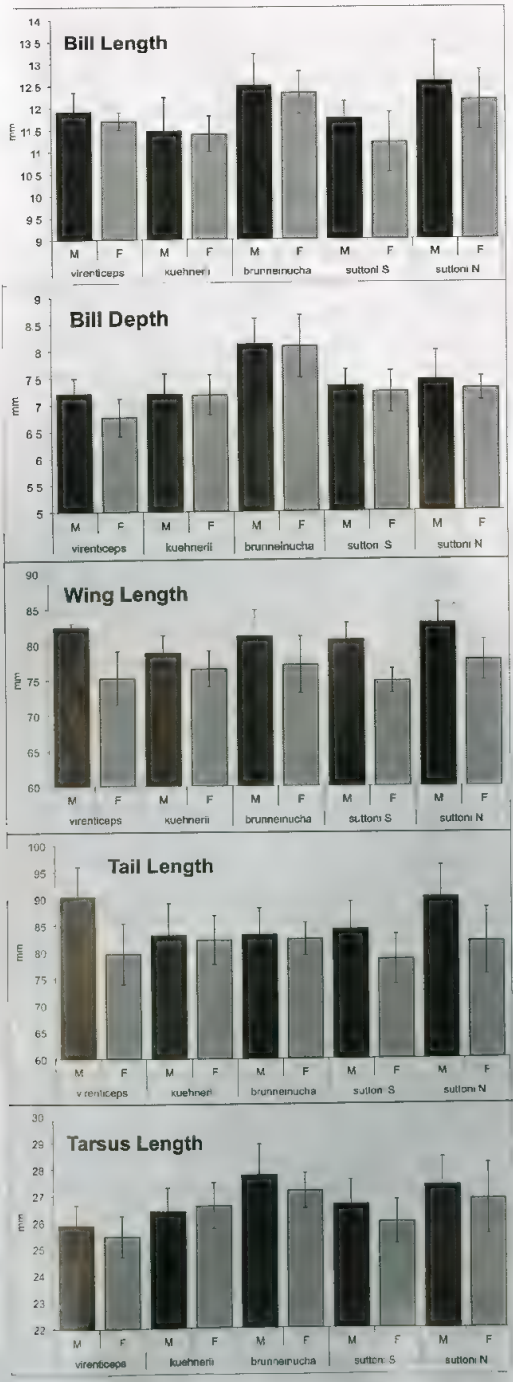

FIG. 4. Mensural comparisons of males and females of four chestnut-capped *Arremon* forms in Mexico, plus *A. virenticeps*, for five mensural characters. "suttoni S" and "suttoni N" refer to samples from southern and northern Oaxaca, respectively. Height of columns indicates the median, and error bars indicate the range observed across all individuals measured.

brunneinucha (Fig. 4). Although discriminant function analyses comparing *A. kuehnerii* with *A. b. suttoni* were statistically significant in both sexes ($P < 0.05$), perhaps indicating some degree of morphometric change, this multivariate approach was nonetheless unable to achieve clear separation of the two (correct classification rates were 83% for males and 80% for females). As such, even in quantitative mensural characters, we see no means of distinguishing unambiguously the new form from *A. b. suttoni* based on external phenotype.

TAXONOMIC RANK

Division of the *Arremon brunneinucha* complex into multiple species initially via recognition of *A. kuehnerii* is warranted on several grounds (Navarro-Sigüenza et al. 2008). First, the traditional (chestnut-crowned) *A. brunneinucha* complex is paraphyletic with respect to the striped-crowned *A. virenticeps*, which is nestled well within the chestnut-crowned populations (Cadena et al. 2007, Navarro-Sigüenza et al. 2008), a relationship that is now strongly supported by our expanded sequence data set. Second, pairs of parapatric populations are highly distinct genetically (Cadena et al. 2007, Navarro-Sigüenza et al. 2008), with no sign of intergradation or introgression, as in the case of *A. b. brunneinucha* and *A. b. suttoni* of the Sierra Madre Oriental (Fig. 1; Navarro-Sigüenza et al. 2008) and likely also for *A. kuehnerii* and *A. brunneinucha*. Finally, overall genetic subdivision in the complex is dramatic, particularly among northern populations, indicating considerable periods of independent evolution by the different populations (Cadena et al. 2007, Navarro-Sigüenza et al. 2008).

Recent taxonomic treatments in ornithology have often had to deal with differential implications under different species concepts (Zink and McKitrick 1995, Remsen 2005), weighing the import of sets of evidence that are emphasized more or less by particular concepts. In the present case, however, these complications are negligible, as the requisites of each concept for species status of *A. kuehnerii* are met. Specifically, for the Phylogenetic Species Concept (de Queiroz and Donoghue 1990, Zink and McKitrick 1995), not just *A. kuehnerii* but all six Mexican forms are clearly diagnosable from one another on the basis of multiple DNA sequence characters, and three are diagnosable based on

unambiguous plumage traits (crown color and presence/absence of breast band); all six forms of this group in Mexico (see Fig. 1) are also reciprocally monophyletic. For the Evolutionary Species Concept (Wiley 1978), the independence of evolutionary trajectories of each of these forms is also clear, as each has fixed multiple unique characters in multiple genes in different sectors of the genome.

The Biological Species Concept (Mayr 1963) focuses on establishment of reproductive isolation among populations—the Mexican populations of montane *Arremon* brush-finches include six distinct forms, of which most are allopatric on different mountain chains, thereby not providing tests of reproductive isolation. However, *A. b. suttoni* and *A. b. brunneinucha* replace one another along the Sierra Madre Oriental within essentially continuous habitat between the Sierra Mazateca (Oaxaca) and the Sierra Madre Oriental (Veracruz and Puebla). Our field experience in this region (Peterson et al. 2003) indicates that no dramatic geographic break separates these populations. Rather, the genetic break between these populations reflects likely reproductive isolation, and these populations provide a test at least of parapatry. As *A. kuehnerii* is similarly differentiated genetically from other lineages in the complex, given this apparent reproductive isolation, recognition of *A. kuehnerii* as a separate species is warranted under the Biological Species Concept.

The possibility that the less-dramatic differentiation of *A. kuehnerii* in nuclear as compared with mitochondrial DNA sequences might reflect ongoing gene flow from *A. b. suttoni* populations to the east appears unlikely, for the following reasons. (1) The dramatic mitochondrial DNA differentiation of this population (Navarro-Sigüenza et al. 2008) indicates that any gene flow would have to be massively sex-biased, with only males moving. (2) The partial nuclear DNA differentiation documented herein indicates some level of sorting among populations, indeed on a level comparable to that in the well-marked *A. virenticeps*. (3) Some degree of phenotypic differentiation can be appreciated from our morphometric results. Finally, (4) allozyme frequency differences previously published (Peterson et al. 1992) included unique alleles (5 alleles at 4 loci) at moderate frequencies in the populations from Guerrero that would be indicative of genetic isolation (Slatkin 1985). All of these lines of evidence argue that gene flow between the brush-finch populations from Guerrero and Oaxaca is negligible. Further indication of no current gene flow is provided by the disjunct nature of the distributional areas of the various groups ... simply put, the distributional areas are discontinuous (Fig. 1), and no easy route exists at present for gene flow to occur.

This particular example—in which cryptic phylogenetic and taxonomic diversity exists without morphological correlates—heralds what is probably vast underestimation of true levels of diversity among birds. That is, as has been pointed out in numerous recent studies and syntheses (Peterson 1998, Lohman et al. 2010, Pratt 2010), true bird diversity likely greatly exceeds the 10,000–12,000 species currently recognized. This study provides yet another example: a phenotypically unmarked (or at best poorly marked) population that turns out to be genetically quite distinct, representing a separate species. Considering the number of bird taxa that show some level of population differentiation across Mexico (Escalante-Pliego and Peterson 1992; Peterson and Navarro-Sigüenza 2000a, b; Navarro-Sigüenza et al. 2001; Sánchez-González et al. 2007), not to mention the Central American cordillera and the Andes chain (Bonaccorso 2009, Sanín et al. 2009, Sedano and Burns 2010, Bonaccorso et al. 2011, Chaves and Smith 2011), we see signals that true bird species diversity will prove much greater than has traditionally been assumed (Mayr 1946).

BIOGEOGRAPHY

The distribution of the chestnut-capped *Arremon* brush-finches along the tropical American cordillera is a classic example of habitat restriction among cloud forest birds (Chapman 1923, Hernández-Baños et al. 1995, Cadena 2007). The mountains of central Guerrero are well known for elevated endemism, both among birds (Peterson and Navarro-Sigüenza 2000b) and in many other taxa (Ramamoorthy et al. 1993). Other bird species endemic to the Sierra Madre del Sur massif of central Guerrero include the jay *Aphelocoma guerrerensis*, the woodcreeper *Xiphocolaptes omiltemensis*, and the hummingbirds *Eupherusa poliocerca* and *Lophornis brachylopha*, although only the latter two are recognized broadly by ornithological authorities (Navarro-Sigüenza and Peterson 2004, Peterson and Navarro-Sigüenza 2009).

Comparisons of phylogeographic patterns across taxa, however, suggest a fair amount of complexity. For instance, whereas the chestnut-capped *Arremon* populations of the Sierra de Yucuñacua of westernmost Oaxaca group with the remaining populations of Oaxaca (Navarro-Sigüenza et al. 2008), populations of *Eupherusa* hummingbirds from Sierra de Yucuñacua are allied with *E. cyanophrys* of the Sierra de Miahuatlán of south-central Oaxaca rather than with *E. poliocerca* of Guerrero or *E. eximia* of northern Oaxaca (Friedmann et al. 1950). More generally, in several phylogeographic studies of other cloud forest birds, populations from Sierra Madre del Sur tend to be distinct from all others, but populations of the Oaxaca and Guerrero portions of the Sierra Madre del Sur (i.e., inclusive of Sierra de Yucuñacua and Sierra de Miahuatlán) tend to be close relatives (e.g., Bonaccorso et al. 2008), a pattern not supported in the present case.

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GEOGRAPHIC VARIATION IN MORPHOLOGY OF DARK-EYED JUNCOS AND IMPLICATIONS FOR POPULATION DIVERGENCE

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ABSTRACT.—Geographic variation in morphology that develops among closely related populations can help drive genetic divergence, and eventually speciation, when those morphological traits are the basis for social interactions that influence reproduction. The North American Dark-eyed Junco (*Junco hyemalis*) complex is an interesting case in speciation. The numerous subspecies have distinct breeding ranges and unique plumage coloration, but based on the presence of hybrid populations and recent genetic data, can be considered to belong to a single species. Research within various populations of juncos has shown first, that wing length and the amount of white on the tail feathers (''tail white'') influence an individual's dominance status and mating success, and second, that these traits can undergo rapid evolution when social and environmental conditions change. Here, I used museum specimens to examine tail white and body size, as measured by wing and tail length, of males and females within and among 13 geographically distinct Dark-eyed Junco subspecies. I documented geographic variation of mean values for each of these morphological traits, as well as patterns of trait co-variation and the degree of sexual dimorphism. I discuss these results in relation to what they may indicate about the generation and maintenance of divergence among the subspecies. *Received 14 November 2012. Accepted 11 February 2013.*

Key words: geographic variation, population divergence, sexual dimorphism, tail white, trait correlation.

There are now several examples of systems in which we suspect we are observing the process of speciation, where over time we can observe changes in morphological, behavioral, and molecular characteristics (e.g., maggot flies, Linn et al. 2003; Galapagos finches, Grant and Grant 2009; Eurasian Blackcaps, *Sylvia atricapilla*, Rolshausen et al. 2009). Such character changes are most often observed between populations that are geographically separated, and they come about through a variety of processes: mutation, drift, and sexual, fecundity, and viability selection. Speciation may progress more rapidly if it involves the divergence of traits that are used in social interactions that determine individuals' survival and reproductive success. For example, variation in mate choice signals can lead to or maintain population divergence through assortative mating (Sætre et al. 1997, Payne et al. 2000, Balakrishnan and Sorenson 2006, Brodin and Haas 2006). In Village Indigobirds (*Vidua chalybeate*), which are inter-specific brood parasites, individuals sometimes parasitize new hosts when they become available after colonization (Payne et al. 2000). Males and females that are born in nests of the new host imprint on that host's song and then a distinct race may form based on assortative mating (Payne et al. 2000). This and other studies highlight the ability to capture population divergence in its early stages. To understand which particular traits are involved in divergence requires detailed study.

The Dark-eyed Junco complex (*Junco hyemalis*) has interested ornithologists for the past century as a study in incipient speciation (Miller 1941, Nolan et al. 2002). One hundred thousand to as early as 10,000 years ago, Dark-eyed Juncos radiated north from the Yellow-eyed Juncos (*Junco phaeonotus*) that reside in Mexico, and have undergone rapid morphological diversification (Milá et al. 2007). Currently in North America, at least six major groups of Dark-eyed Juncos (white-winged, red-backed, gray-headed, slate-colored, pink-sided and Oregon), and many subspecies within these groups, are readily recognized based on their breeding ranges and plumage variation, such as the presence or absence of a dark hood, buff side coloration, and the overall body color (Miller 1941, Nolan et al. 2002). Despite some distinguishing characteristics, molecular data and the presence of hybrid populations are evidence that the subspecies are not reproductively isolated (Miller 1941, Milá et al. 2007). In this study, I examined geographic variation in socially selected morphological traits within and among junco subspecies, since evidence for divergence in those traits could indicate potential for further diversification within the species complex.

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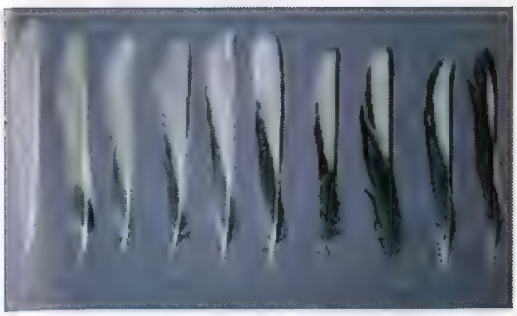


FIG. 1. Image of junco tail feathers (a mix of rectrices 4–6) showing variation in tail white. The proportion of white was estimated in increments of one-tenth of a feather ranging from 1.0 (far left) to 0.1 (far right) that is white.

The study of juncos as a whole suggests that at least two traits are subject to selection in males: wing length and the proportion of white on the otherwise gray tail feathers (''tail white''; Fig. 1). Wing length relates to dominance; in contests over food, males with longer wings are dominant to both smaller males and females, who on average have shorter wings than males (*J. h. montanus,* Balph et al. 1979; *J. h. hyemalis,* Holberton et al. 1989; *J. h. hyemalis,* Ketterson 1979; *J. h. pinosus,* EDF, unpubl. data). Tail white can also affect male dominance interactions. In wintering juncos, males with whiter tails dominated duller males, although tail white was not as strong a predictor of dominance as was wing length and plumage darkness (*J. h. montanus,* Balph et al. 1979; *J. h. hyemalis,* Ketterson 1979). In another study, natural tail white did not influence social dominance in wintering juncos, while wing length and plumage darkness did (*J. h. pinosus,* EDF, unpubl. data). Finally, males whose body plumage was experimentally darkened and tails enhanced with white were able to dominate un-manipulated males, but because the body and tail were manipulated simultaneously, the relative importance of the traits could not be determined (*J. h. hyemalis,* Holberton et al. 1989).

Male tail white could also be a signal used in mate choice. Males perch and then slowly spread their tail feathers to display the white portions to females (*J. h. carolinensis,* Enstrom et al. 1997; *J. h. thurberi,* Yeh 2004; EDF, pers. obs.), and females in aviary mate choice studies preferred males with whiter tails (*J. h. carolinensis,* Hill et al. 1999, McGlothlin et al. 2004). Males, on the other hand, did not show a preference for tail-white enhanced females in a similar experiment (*J. h. carolinensis,* Wolf et al. 2004). Consistent with the idea that tail white is sexually selected in males but not females, males in all junco subspecies on average have more white on their tails than do females (Miller 1941). In summary, to the degree that dominance influences survival, wing length and to a lesser extent, tail white, are subject to viability selection in at least some junco populations through dominance interactions over food. Additionally, to the extent that attractiveness influences mating success, tail white appears to be subject to sexual selection in some populations.

Tail length is also of interest in studying morphological variation in Dark-eyed Juncos. In *J. h. carolinensis*, tail length predicts female lifetime reproductive success via fecundity selection; females with longer tails have greater fecundity (McGlothlin et al. 2005). This relationship may come about if tail length relates to overall body size. Relatively large females could have the most energy to invest in reproduction, although in some cases smaller females may be more successful if they can easily accumulate resources for egg laying (Downhower 1976, Calder 1984, Pincheira-Donoso and Tregenza 2011). I also included tail length in this study to examine the possibility that the proportion of white on the tail is related to the tail's length, i.e., that longer tails are also whiter. This could occur, for instance if tail length and tail white are both influenced by an individual's condition or quality or if the development of tail white relates to the growth process of the feathers themselves (McGlothlin et al. 2007).

When historical, environmental, and social conditions vary geographically, trait divergence among populations is likely to occur. If traits like wing length, tail white, and tail length in Dark-eyed Juncos have the potential to influence mating success, survival, and fecundity within populations, then their divergence could over time increase reproductive isolation among the junco subspecies. Geographic variation in wing and tail length was documented extensively by Miller (1941), but quantitative descriptions of tail white are available for only two of the 13 Dark-eyed Junco subspecies (*J. h. carolinensis,* Hill et al. 1999; *J. h. thurberi,* Yeh 2004; Ferree 2007). I used museum specimens to quantify the extent of tail white of the other Dark-eyed Junco subspecies and two subspecies of Yellow-eyed Juncos, their sister group. I also compared the strength of the

correlation between individuals' wing length, tail length, and tail white for males and females, and the degree of sexual dimorphism of these traits within each subspecies.

Sometimes selection acts to correlate particular traits. In the most thoroughly studied junco subspecies, *J. h. carolinensis,* sexual selection most strongly favored males with longer wings and more tail white, (McGlothlin et al. 2005). Males in which tail white and wing length are not correlated were selected against, such as if a male with long wings had little white and vice-versa (McGlothlin et al. 2005). One explanation for this correlation is that longer wings provide a competitive advantage among males, and whiter tails enhance mate attraction, but both traits could also attract more rivals and conspecific aggression (McGlothlin et al. 2005). The implications from this study are that wing length and tail white may be correlated in populations where particular trait combinations are favored by correlational selection, but that they may evolve independently under different selection regimes or environmental conditions, as recently seen in another junco subspecies. A population of *J. h. thurberi* that previously only wintered in San Diego, lower in elevation than its mountainous summer range, about 40 years ago began breeding there and has undergone rapid evolution in tail white but less so in body size. In relation to its founding population, tail white in the San Diego population has decreased by about 20%, while wing length and tail length only decreased by about 4% (Rasner et al. 2004, Yeh 2004). The reduction in tail white is likely because of a shift from a short breeding season with a competitive social environment to a mild climate that is less so (Price et al. 2008). In this example, variation in the correspondence of body size and tail white among populations could indicate varying environmental or social conditions, which in turn contributes to population divergence.

Sexual dimorphism is also a phenomenon that can carry the signature of selection. For example, it is usually considered evidence that sexual selection acts to display or enhance the ability of individuals of one sex, normally males, to compete with their rivals or to attract mates (Price 1984). Among species of shorebirds, gulls, and alcids with different types of mating systems, for example, sexual dimorphism in body size is greater in socially polygynous species than in less polygynous species (Székely et al. 2000). Sexual dimorphism can arise for other reasons, such as niche differentiation in relation to foraging, as seen in anolis lizards (*Anolis conspersus*, Schoener 1967) and species of hermit hummingbirds (Phaethornithinae, Temeles et al. 2010). Geographic variation in the degree of trait dimorphism, like variation in the extent of trait correlation described above, could therefore provide evidence that populations are on different evolutionary trajectories. For example, in European Barn Owl females are more reddish-brown and spotted than males, and the degree of dimorphism increases from north to south (*Tyto alba*, Roulin 2003). This variation is likely because of geographic variation in directional selection but also in sex-specific selection for phenotypic correlation of the two plumage traits in males (Roulin 2003). House Finches (*Carpodacus mexicanus*) have been well studied in relation to geographic variation in sexual dimorphism; males vary geographically in how bright they are relative to females, largely because of geographic variation in the carotenoid content of their food (Hill 1994). Again, geographic variation in sexual dimorphism could indicate variation among the subspecies in social or environmental conditions that influence trait expression and evolution in males and females. In summary, this study identifies ways in which the Dark-eyed Junco subspecies have diverged from each other, thus establishing the basis for further research into the factors accounting for and implications of variation in trait expression among the junco subspecies.

METHODS

Measurement of Museum Specimens.—I measured wing length, tail length, and tail white on specimens at the Museum of Vertebrate Zoology at the University of California Berkeley (Apr 2003 and Feb 2007; all subspecies except *J. h. carolinensis*), the Cornell University Museum of Vertebrates (Apr 2007; *J. ph. phaeonotus, J. ph. palliatus, and J. h. oreganus*), and the Museum of Comparative Zoology at Harvard University (Aug 2007; *J. h. carolinensis*). I examined male and female specimens from 13 Dark-eyed Junco subspecies and two Yellow-eyed Junco subspecies that were initially captured during breeding seasons between 1874 and 1947 (Table 1; Fig. 2).

I measured wing chord and tail length (from oil gland to tail tip) using a ruler to an accuracy of 0.5 mm. To determine whether the wing and tail data accurately reflected the true size of the birds

TABLE 1. Names and sample sizes for each Dark-eyed Junco subspecies measured, as well as two subspecies of Yellow-eyed Junco. Fewer female than male specimens were available.

Common name of major subspecies	Subspecies	Male *n*	Female *n*
White-winged Junco	*J. h. aikeni*	39	17
Red-backed Junco	*J. h. dorsalis*	24	9
Gray-headed Junco	*J. h. caniceps*	40	18
Slate-colored Junco	*J. h. carolinensis*	54	24
	J. h. cismontanus	38	20
	J. h. hyemalis	30	25
Pink-sided Junco	*J. h. mearnsi*	38	18
Oregon Junco	*J. h. montanus*	41	18
	J. h. oreganus	37	18
	J. h. pinosus	40	22
	J. h. shufeldti	22	18
	J. h. thurberi	35	25
	J. h. townsendi	23	16
Yellow-eyed Junco	*J. ph. palliatus*	14	7
	J. ph. phaeonotus	19	9
	Total	494	264

soon after they were collected, I compared the mean wing and tail length values I obtained for each subspecies to those published by Miller (1941), who measured wing chord and tail length in the same way as I did and on the same birds. Miller (1941) reported higher values than me, because specimens I used were dessicated since they were collected around 1900 (Winker 1993). My comparison of mean and SD in Statistica (StatSoft, Inc. Tulsa, OK, USA) found that 7/12 and 11/12 comparisons were significant for wing length and tail length respectively. Based on the average percentage difference between the observed and expected mean wing and tail lengths among the subspecies, I added a correction factor of 1.7% to each wing measurement and 3% to each tail measurement to account for shrinkage. These adjustments were consistent with those reported in the literature for other species (17 bird species; Winker 1993).

I estimated tail white following methodology used in previous studies (Holberton et al. 1989, Hill et al. 1999, Ferree 2007). On each tail feather, I estimated the proportion of white in tenths of a feather, from 1.0 being completely white to 0 as having no white (Fig. 1). I calculated a total tail white score as the sum of the amount of white on each feather from the two sides of the tail. Most juncos have white on the three outer tail feathers (rectrices 4–6), with the most variation on the third feather in (rectrix 4). Some subspecies have white even on the fourth rectrices, while others have white on only the outer two rectrices. As an example of how I created a final tail white score, if on both the right and left sides of the tail the outer two feathers were completely white and the third was half white, that individual would have a total of five white feathers (2.5 on each side), out of the 12 feathers on the tail. I verified the reliability of this method by estimating tail white on 30 museum specimens on 3 separate days and then by calculating the within-individual repeatability of their tail white scores (repeatability = 95.8%, $P < 0.001$; Lessels and Boag 1987). Finally, tail white scores based on visual estimation are highly correlated with those estimated using digital photography technology ($r > 0.90$, J.W. Atwell, pers. comm.; Yeh 2004).

I calculated sexual dimorphism for a given trait as the ratio of the mean male value over the mean female value for each subspecies (Webster 1992, Greenwood 2003). I took the natural log (ln) of the ratios when included in analyses to account for problems associated with the non-normal distribution of ratios (Webster 1992).

Finally, tail white, wing length, and tail length could increase with an individual's age. In two subspecies, tail white increased by about 3–4% as individuals aged from yearlings to second years, but not thereafter (*J. h. thurberi*, Yeh 2004; *J. h. carolinensis*, Wolf et al. 2004). Wing and tail lengths did not increase substantially in at least one population of *J. h. thurberi* (Miller 1941). Information on age, however, was not available

FIG. 2. Locations at which Dark-eyed Junco specimens were originally collected between 1887 and 1949 (now housed at Museum of Vertebrate Zoology, University of California Berkeley, the Cornell University Museum of Vertebrates, and the Museum of Comparative Zoology at Harvard University). Yellow-eyed Juncos were collected in Mexico.

for the specimens measured in this study, nor was age accounted for by Miller (1941). Given that the specimens were probably of mixed breeding ages and that small variation occurs only between the first and second year, variation because of age likely did not have a large impact on the results.

Statistical Analyses.—I evaluated whether the dependent variables met the assumption of normality by visual inspection of a frequency diagram and the Shapiro-Wilk test. I also tested for homogeneity of variances using Levene's test. Except for the ln-transformation of the sexual dimorphism ratios mentioned above, no adjustments were needed based on these assessments. I then conducted three series of analyses to examine: (1) geographic variation in trait means, (2) the relationships among wing length, tail length, and tail white among and within the subspecies, and (3) sexual dimorphism among the subspecies.

First, I assessed whether there was significant variation in wing length, tail length, and tail white among the Dark-eyed Junco subspecies using univariate general linear models (GLM) with each measurement as a dependent variable and subspecies, sex, and their interaction as fixed factors. If the interaction between subspecies and sex was not significant and significant differences occurred between males and females, I analyzed the sexes separately to test for differences among the subspecies. I used Tukey HSD post-hoc tests to determine which Dark-eyed Junco subspecies differed from each other to identify clusters of subspecies that were similar to each other in each

trait. In the figures, but not analyses, I also included the mean measurements for the Yellow-eyed Junco subspecies for comparison with those of the Dark-eyed Junco subspecies.

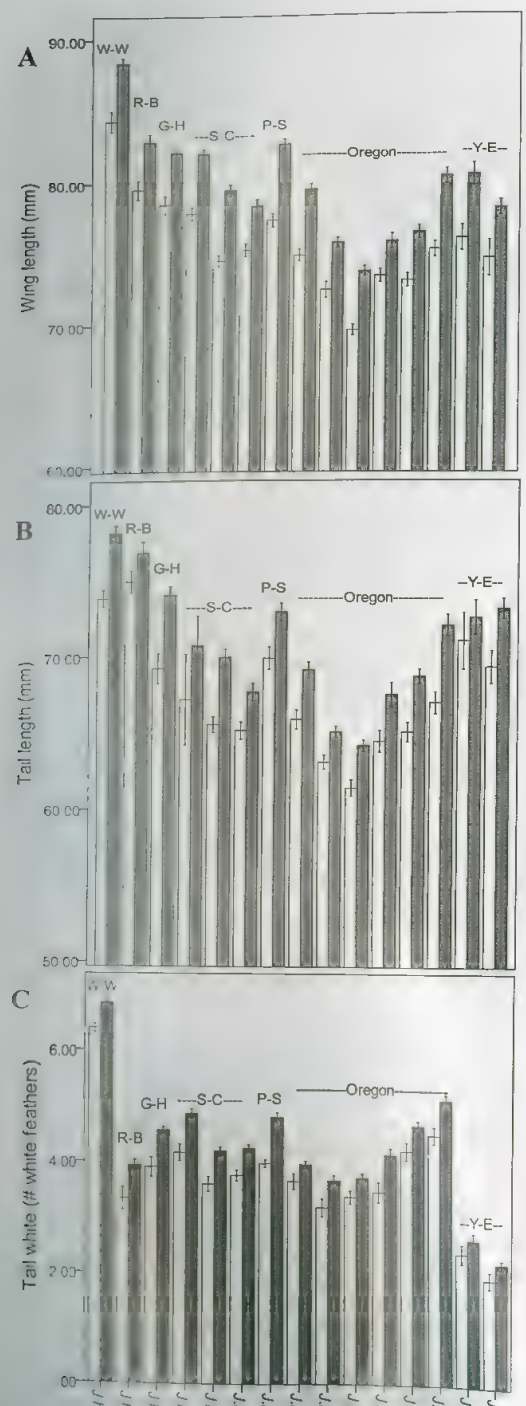
With regression, I tested the strength of the relationship between wing length and tail length and between tail white and measures of body size, first for males and females of all dark-eyed subspecies combined. Using an ANCOVA, I then examined these relationships for each sex within each subspecies. Specifically, I used the interaction factor between subspecies and the covariate to determine if the relationship between a given pair of traits varied significantly among the groups. If the interaction effect was not significant (the slopes were relatively equal), I was then interested in whether individual subspecies deviated from the overall pattern across individuals. In particular, I calculated the unstandardized residuals from regressions of one trait on another to test if some subspecies, for example had more or less tail white than expected given their body size, which could be true even if the slopes did not differ among subspecies. With a univariate GLM, I then determined whether the residuals for each subspecies were significantly different from each other, with Tukey HSD post-hoc tests as follow-up to significant main effects. I also included the two Yellow-eyed Junco subspecies in these analyses.

Lastly, I compared the degree of sexual dimorphism in each Dark-eyed Junco subspecies visually using a bar chart, again including the Yellow-eyed Junco for comparison. I also tested the hypothesis that selection for absolute size could be associated with greater sexual dimorphism among the Dark-eyed Junco subspecies; I used regression to examine the relationship between the subspecies' wing length dimorphism and mean male wing length, tail length dimorphism, and mean male tail length, and tail white dimorphism and mean male tail white. Finally, I asked whether dimorphism in one trait was correlated with dimorphism in another trait (wing length, tail length, or tail white). Analyses were conducted in SPSS 19.0 (SPSS Inc. 2011), were two-tailed, and used 0.05 as the cut-off for significance. I presented means with standard errors.

RESULTS

Morphological Variation Among Subspecies.—Measurements of wing and tail length supported Miller's (1941) findings of significant variation among the subspecies (Wing: males, $F_{12,449} = 105.39$, $P < 0.001$; females, $F_{12,235} = 54.39$, $P < 0.001$; Tail: males, $F_{12,446} = 60.89$, $P < 0.001$; females, $F_{12,234} = 32.49$, $P < 0.001$; Fig. 3A, B). Tail white also varied significantly among the subspecies ($F_{12,417} = 85.00$, $P < 0.001$; females, $F_{12,215} = 23.00$, $P < 0.001$; Fig. 3C). Based on post-hoc tests, the subspecies fell into a few distinct subsets (Fig. 3; see Acknowledgments to access Appendix Tables 1–3 in *Dryad*). In both sexes, *J. h. aikeni* had the longest wing and most tail white of all subspecies, but was joined by *J. d. dorsalis* for having the longest tails (Fig. 3; see Acknowledgments to access Appendix Tables 1–3 in *Dryad*). On the other end of the spectrum, *J. h. pinosus* males and females had the shortest wings of all of the dark-eyed subspecies, but grouped with a few other geographically dispersed subspecies in relation to tail length and tail white (*J. h. dorsalis, J. h. montanus, J. h. oreganus;* Fig. 3; see Acknowledgments to access Appendix Tables 1–3 in *Dryad*). In all three traits, there were more significant differences among the males of different subspecies than among the females (see Acknowledgments to access Appendix Tables 1–3 in *Dryad*).

Trait Correlation Among and Within Subspecies.—The three dependent variables were significantly correlated across all individuals: larger individuals had whiter tails and birds with longer wings had longer tails (Table 2; Fig. 4A–C). The slopes of the relationships between each pair of variables were not significantly different among the subspecies for either sex (based on subspecies by covariate interactions; Table 3). Although each pair of the dependent variables was positively correlated across individuals of all subspecies and the slopes did not differ among the groups, these relationships were not always significant within each subspecies (Table 2). Only in male *J. h. aikeni* were tail and wing length significantly correlated as well as tail white and both measures of body size: as wing and tail length increased, so did the proportion of white on the tail feathers (Table 2). In several other subspecies, males with longer wings also had longer tails (*J. h. caniceps, J. h. carolinensis, J. h. cismontanus, J. h. hyemalis, J. h. mearnsi, J. h. montanus, J. h. pinosus, J. h. shufeldti,* and *J. h. townsendi*), but within no other subspecies was tail white positively related to either measure of body size (Table 2). Wing length and tail length were also correlated among females of five subspecies (*J. h. dorsalis, J. h.*



caniceps, J. h. cismontanus, J. h. mearnsi, and *J. h. thurberi*), but female body size and tail white were not correlated within any one of the subspecies (Table 2). In two subspecies, wing and tail length were significantly correlated in females but not males (*J. h. dorsalis* and *J. h. thurberi*; Table 2).

I was then interested in the degree to which some subspecies deviated from the positive covariation of the traits that was seen among individuals of all subspecies combined. I used the unstandardized residuals from the regressions of tail length on wing length, and tail white on wing and tail length to determine if individuals within some subspecies had more tail white than expected for their body size or were larger in one aspect of body size than another (Fig. 5). Overall, the mean residuals for all pairs of traits varied significantly among the subspecies (Tail white/Wing length residual: males, $F_{14,460} = 24.76$, $P < 0.001$; females, $F_{14,225} = 13.83$, $P < 0.001$; Tail white/tail length residual: males, $F_{14,477} = 8.63$, $P < 0.001$; females, $F_{14,247} = 5.33$, $P < 0.001$; Tail length/wing length residual: males, $F_{14,459} = 30.25$, $P < 0.001$; females, $F_{14,216} = 27.79$, $P < 0.001$; see Acknowledgments to access Appendix Tables 4–6 in *Dryad*). In particular, both male and female *J. h. aikeni* had more tail white than expected for their body size (Fig. 5; see Acknowledgments to access Appendix Tables 4, 5 in *Dryad*). Male and female *J. h. dorsalis* and *J. h. carolinensis* on the other hand, tended to have less tail white than expected for their body size, as did the Yellow-eyed Junco subspecies (Fig. 5). The other striking pattern seen in *J. h. dorsalis* (and the Yellow-eyed Juncos) was that males and females had longer tails than predicted by their wing lengths (Fig. 5; see Acknowledgments to access Appendix Table 6 in *Dryad*).

Sexual Dimorphism.—Males had longer wings and tails and more tail white than females in all subspecies (mean wing ratio = 1.05 ± 0.003, mean tail ratio = 1.05 ± 0.004, mean tail white

←

FIG. 3. Mean (± SE) A) wing length, B) tail length, and C) tail white in females (white) and males (shaded) in each Dark-eyed Junco subspecies, also grouped into the major subspecies (White-winged (W-W), Red-backed (R-B), Gray-headed (G-H), Slate-colored (S-C), Pink-sided (P-S), Oregon), with the two subspecies of Yellow-eyed Juncos (Y-E) for comparison. See Table 1 for sample sizes.

TABLE 2. Correlations among the dependent variables, tail length, wing length, and tail white in males and females of each Dark-eyed Junco subspecies. Only significant correlations ($P \leq 0.05$) are shown. See Table 1 for sample sizes.

	Tail/wing	Tail white/tail	Tail white/wing
	r	*r*	*r*
All individuals			
Male	0.78***	0.51***	0.60***
Female	0.76***	0.39***	0.54***
J. h. aikeni			
Male	0.60***	0.38*	0.36*
Female	0.32	−0.14	0.46
J. h. dorsalis			
Male	0.37	−0.06	−0.12
Female	0.73*	0.31	0.06
J. h. caniceps			
Male	0.36*	0.23	−0.12
Female	0.52*	0.21	0.40
J. h. carolinensis			
Male	0.45**	0.12	0.19
Female	0.07	−0.05	0.51
J. h. cismontanus			
Male	0.49***	0.30	0.26
Female	0.44*	0.20	0.03
J. h. hyemalis			
Male	0.40*	0.11	0.06
Female	0.38	0.03	0.25
J. h. mearnsi			
Male	0.41**	−0.15	−0.01
Female	0.52*	−0.10	−0.02
J. h. montanus			
Male	0.57***	−0.03	0.18
Female	0.30	−0.21	0.42
J. h. oreganus			
Male	0.20	0.04	0.24
Female	0.44	0.20	0.09
J. h. pinosus			
Male	0.36*	0.33	0.22
Female	0.37	−0.05	0.40
J. h. shufeldti			
Male	0.57**	0.17	0.16
Female	0.42	0.12	0.17
J. h. thurberi			
Male	0.30	−0.18	−0.09
Female	0.40*	0.41	0.34
J. h. townsendi			
Male	0.49*	0.24	0.24
Female	0.44	0.23	0.33

*** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$

TABLE 3. Significance of interaction term (subspecies * covariate interaction) from an ANCOVA including subspecies as a fixed factor, wing length or tail length as the covariate, and tail white or tail length as the dependent variable.

Dependent variable	Significance of interaction term (subspecies * covariate)
Tail white	**Subspecies * Wing length**
Male	$F_{14,431} = 0.95$, $P = 0.50$
Female	$F_{14,200} = 0.44$, $P = 0.96$
Tail white	**Subspecies * Tail length**
Male	$F_{14,428} = 1.66$, $P = 0.061$
Female	$F_{14,201} = 0.51$, $P = 0.92$
Tail length	**Subspecies * Wing length**
Male	$F_{14,462} = 0.86$, $P = 0.60$
Female	$F_{14,231} = 0.89$, $P = 0.56$

ratio = 1.14 ± 0. 01; Fig. 6). While no statistical tests could be used to compare the ratios among the subspecies, the small standard errors indicated that they had roughly equal degrees of sexual dimorphism in wing length and tail length (Fig. 6). Tail white was more dimorphic in some subspecies than others; most notably there was less sexual dimorphism in *J. h. aikeni* and *J. h. montanus* than in the other subspecies (tail white ratio of male/female = 1.07), while *J. h. mearnsi* had the greatest difference between mean male and female tail white (tail white ratio of male/female = 1.21).

Among the subspecies, the degree of dimorphism in a given trait was not related to the mean magnitude of that trait. For example, subspecies in which males had longer wings did not have greater sexual dimorphism in wing length ($R^2 = 0.02$, $F_{1,11} = 0.18$, $P = 0.68$). Similarly, tail length dimorphism and tail white dimorphism were not related to the mean tail length or tail white, respectively, of a species (tail length: $R^2 = 0.03$; $F_{1,11} = 0.38$, $P = 0.55$; tail white: $R^2 = 0.10$, $F_{1,11} = 1.24$, $P = 0.29$).

For the most part, dimorphism in one trait was not significantly correlated with dimorphism in another trait, although dimorphism in tail length tended to be positively related to dimorphism in wing length (correlation of tail length and wing length dimorphism, $r = 0.43$, $P = 0.14$, $n = 13$; correlation of tail white and wing length dimorphism, $r = 0.07$, $P = 0.83$, $n = 13$; correlation of tail white and tail length dimorphism, $r = 0.17$, $P = 0.57$, $n = 13$)

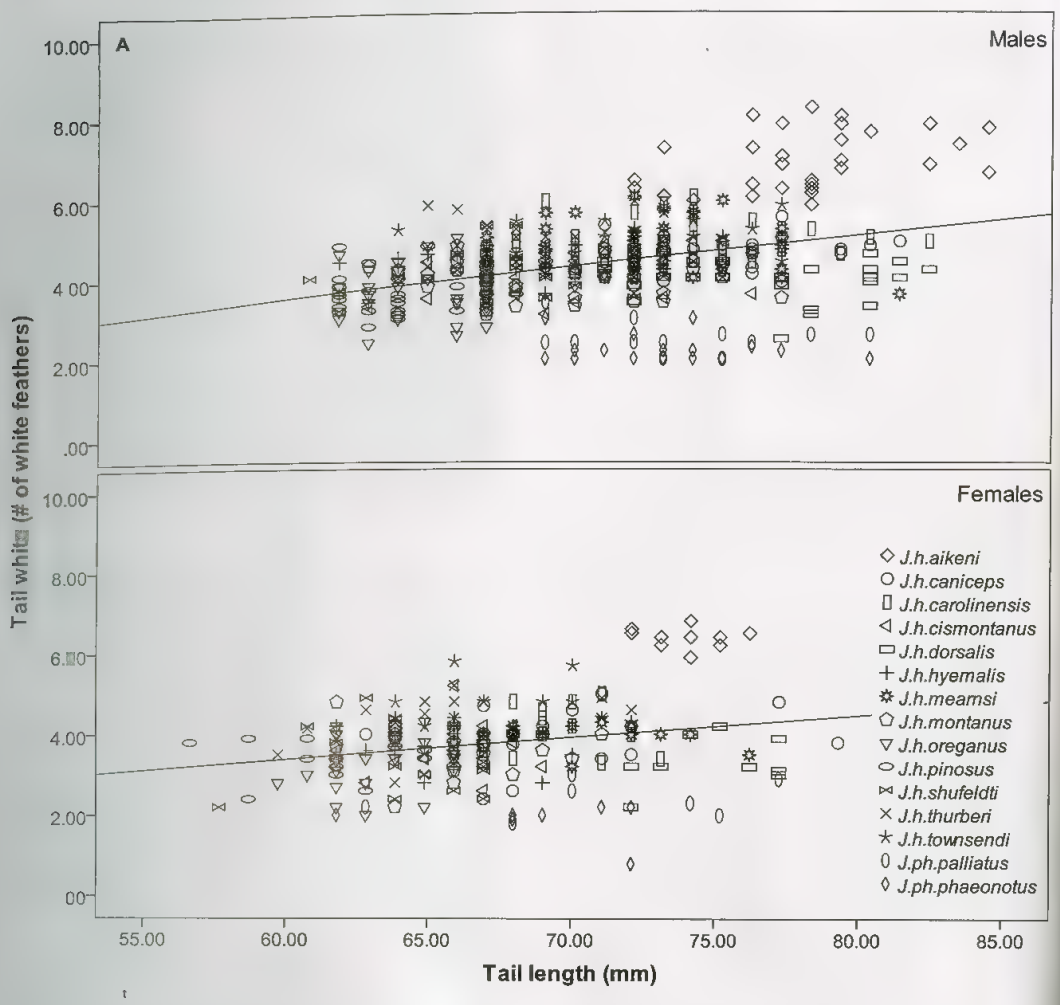


FIG. 4. Relationship between A) tail white and tail length, B) tail white and wing length, and C) tail length and wing length in all male (n = 459) and female (n = 229) Dark-eyed Juncos.

DISCUSSION

The purpose of this study was to examine ways that subspecies within the Dark-eyed Junco complex have diverged morphologically in traits shown to be influenced by both social and environmental conditions. Specifically, I examined variation in wing length, tail length, and tail white, each previously shown to be under selection in at least one junco population. Besides variation in the mean values of these traits, I also considered how they may be correlated and the degree of dimorphism among and within subspecies. The evidence I found for such divergence will provide insight for future studies examining the developmental and evolutionary mechanisms underlying diversification within this lineage.

Morphological Variation Among Subspecies.—Based on the measurements taken in this study, and as was known from earlier studies, the junco subspecies differ significantly in wing and tail lengths (Miller 1941; Fig. 3). Previously unavailable was a quantitative comparison among the many junco subspecies of the proportion of the tail feathers that are white (see Miller 1941 for qualitative descriptions; see Yeh 2004 for comparison of populations within *J. h. thurberi*). Here, I show that to an even greater degree than variation in wing and tail length, Dark-eyed Junco

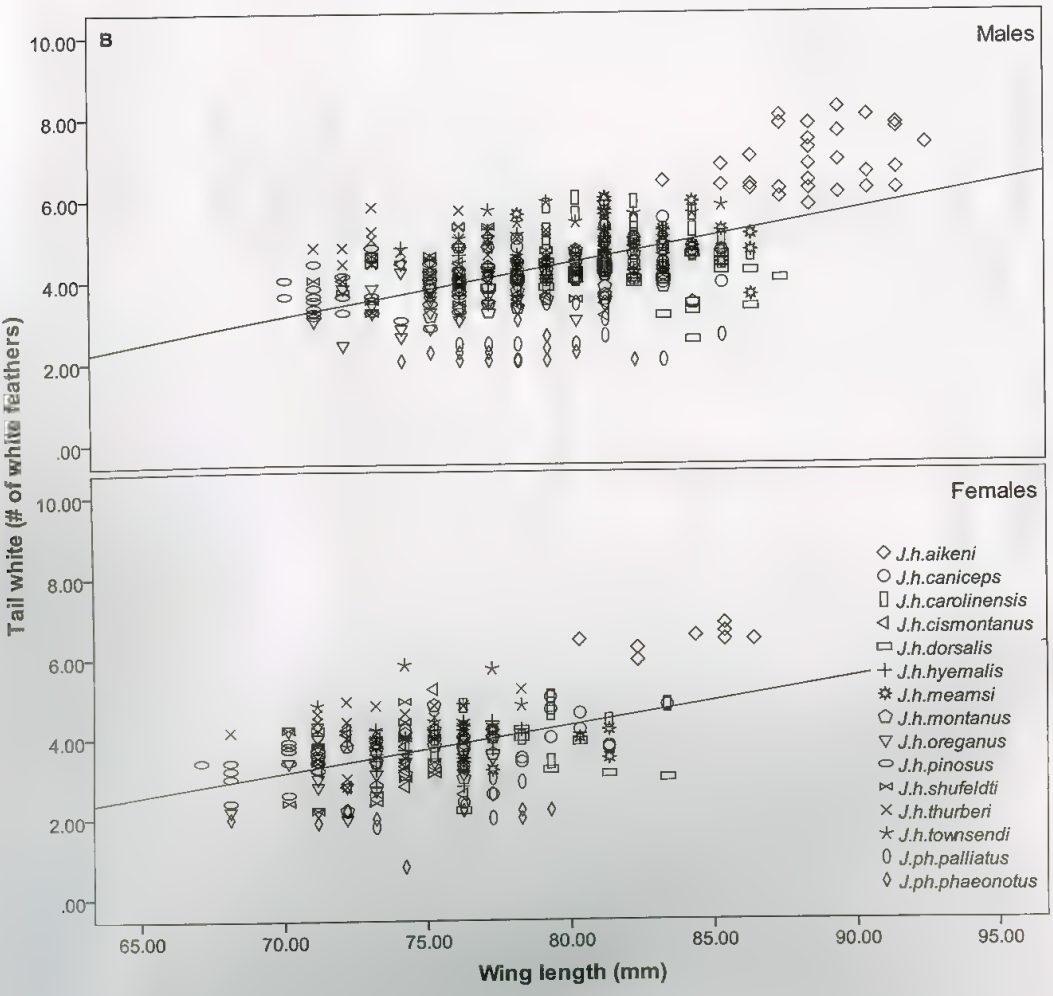


FIG. 4. Continued.

subspecies show considerable variation in tail white (Fig. 3). Studies investigating determinants of body size or tail white within one subspecies could help shed light on why these traits vary among the junco subspecies.

Climate, which varies with habitat, latitude, longitude, and elevation, is one variable that could influence the expression of trait morphology. Miller (1941) found that junco body size was, with some exceptions, positively correlated with latitude and elevation, and the extent of white on the tail was negatively correlated with humidity (Miller 1941, Nolan et al. 2002). Within California, the tails of *J. h. thurberi* become brighter with increasing latitude (Yeh 2004). Environmental conditions could relate to these traits because of their influence on social conditions. The White-winged Junco, *J. h. aikeni*, for example, stood out as having the longest wings and the most tail white of all of the junco subspecies, possibly because of intense selection on males due to a short breeding season in the range of this subspecies (South Dakota). In areas with short breeding seasons and sometimes harsh conditions, competition could favor larger individuals and those with the brightest tails (*J. h. montanus,* Balph et al. 1979; *J. h. hyemalis,* Holberton et al. 1989; *J. h. carolinensis,* Ketterson 1979). Within *J. h. thurberi*, the effect of habitat and its associated climate have been observed first-hand. When a population of juncos from the mountains of southern California started breeding in San Diego,

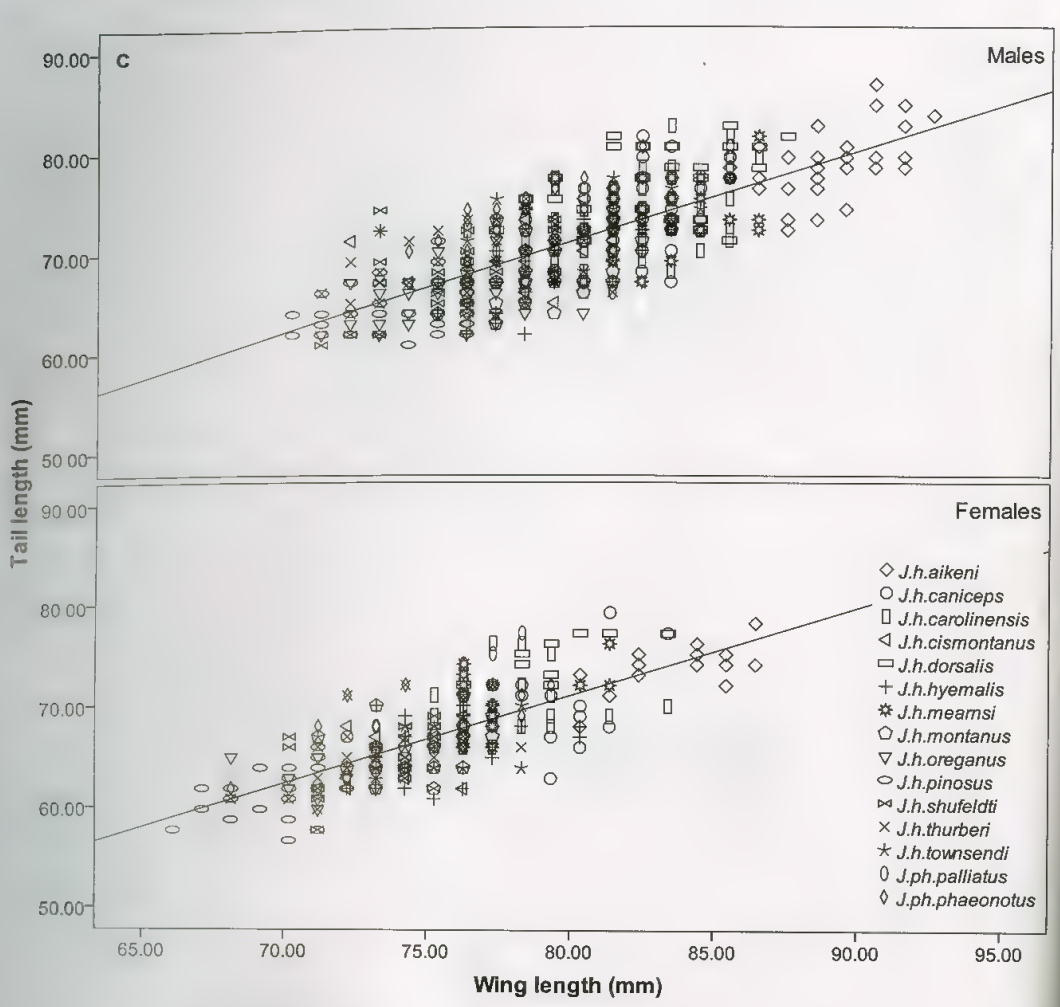


FIG. 4. Continued.

California, along the coast, the mean tail white of that new population was reduced by 24% over only a few generations (Yeh 2004), while wing length also declined, but to a much lesser degree (Rasner et al. 2004). Researchers concluded that the milder climate in the coastal population compared to the mountain population was associated with a longer, less competitive breeding season that led to a reduction in tail white and body size, (*J. h. thurberi;* Rasner et al. 2004, Yeh 2004, Yeh and Price 2004, Price et al. 2008). Also consistent with a role of climate in explaining trait magnitude, the smaller size and duller tails of *J. h. pinosus* and *J. h. oreganus*, found along the central California coast, could result from relaxed selection in a climate that creates a long breeding season and mild year-round conditions. Studies that examine the relationship between correlates of climate, like latitude or elevation, and tail white across the junco subspecies will be useful in explaining the geographic variation observed.

Mechanistically, testosterone and variability in diet could influence the observed variation in trait expression; testosterone is positively related to aggressive behaviors and negatively related to parental care behaviors (*J. h. carolinensis*; Ketterson and Nolan 1992). Testosterone is also positively correlated with male tail white within *J. h. carolinensis* (McGlothlin et al. 2008). A similar relationship between testosterone and tail white is seen in *J. h. thurberi;* compared to its nearby ancestral population, the San Diego

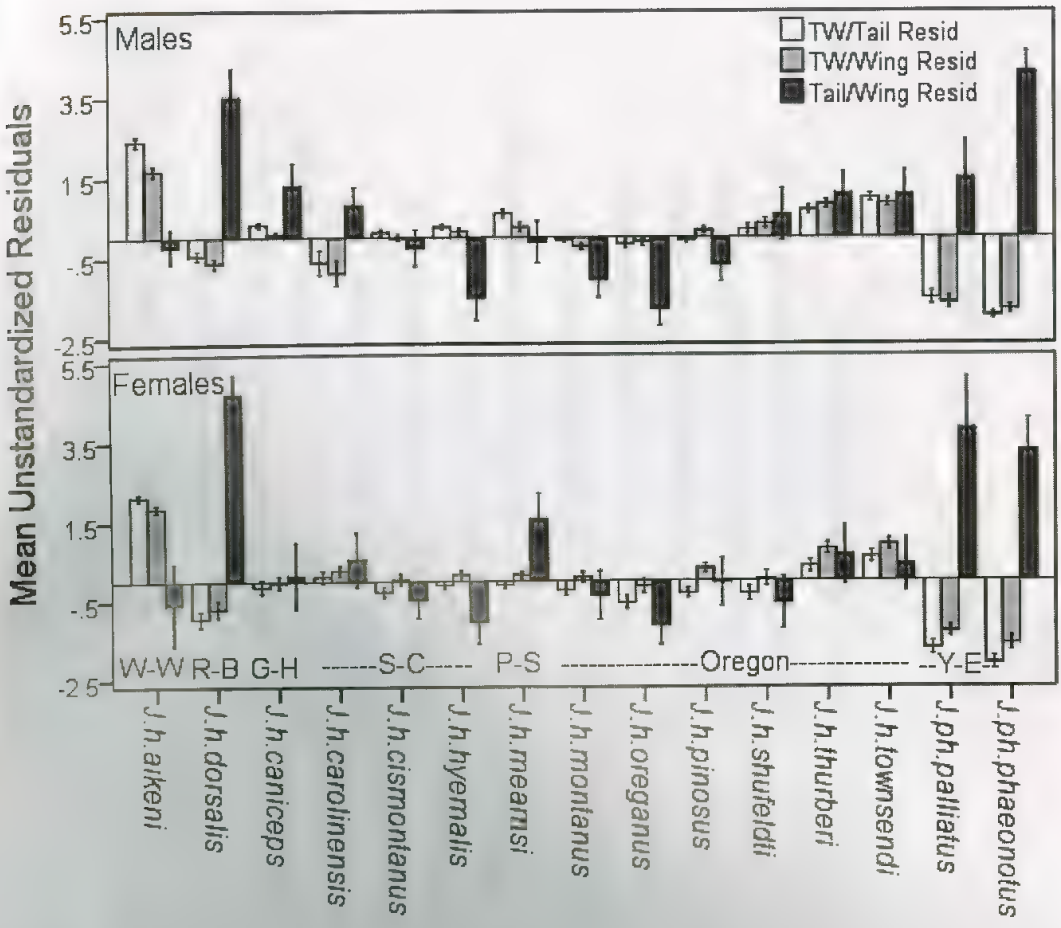


FIG. 5. Mean unstandardized residuals (± SE) from regression of tail white (TW) on tail length (Tail), tail white on wing length (Wing), and tail length on wing length for males and females of each Dark-eyed Junco subspecies, also grouped into the major subspecies (White-winged (W-W), Red-backed (R B), Gray-headed (G-H), Slate-colored (S-C), Pink-sided (P-S) and Oregon) with the two subspecies of Yellow-eyed Juncos (Y-E) for comparison. See Table 1 for sample sizes.

population of *J. h. thurberi* lives in a milder climate with a longer breeding season, and males have reduced peak testosterone and less tail white (J. W. Atwell et al., unpubl. data). Further investigation of the relationship between testosterone and tail white, and how selection acts on behaviors mediated by testosterone could help explain geographic variation in this trait. Access to food also has a direct influence on wing length and the amount of tail white expressed, at least in individuals kept in captivity (*J. h. hyemalis,* Bears et al. 2008; *J. h. carolinensis,* McGlothlin et al. 2007). The abundance and quality of food could also vary geographically and influence trait expression and evolution among the Dark-eyed Junco subspecies.

Trait Correlation Among and Within Subspecies.—The degree of correlation between traits can also provide some insight into how selection is acting in the population. For example, in many species, large males are also the most ornamented (Doucet and Montgomerie 2003, Kodric-Brown et al. 2006). The reasons for the covariation of traits are many: they could be genetically correlated, the same type of selection, like sexual selection, could act on both of them, or they could be co-favored through distinct mechanisms (for example via sexual and viability selection). Understanding how certain traits relate to each other among and within the junco subspecies can help highlight ways that they might be diverging.

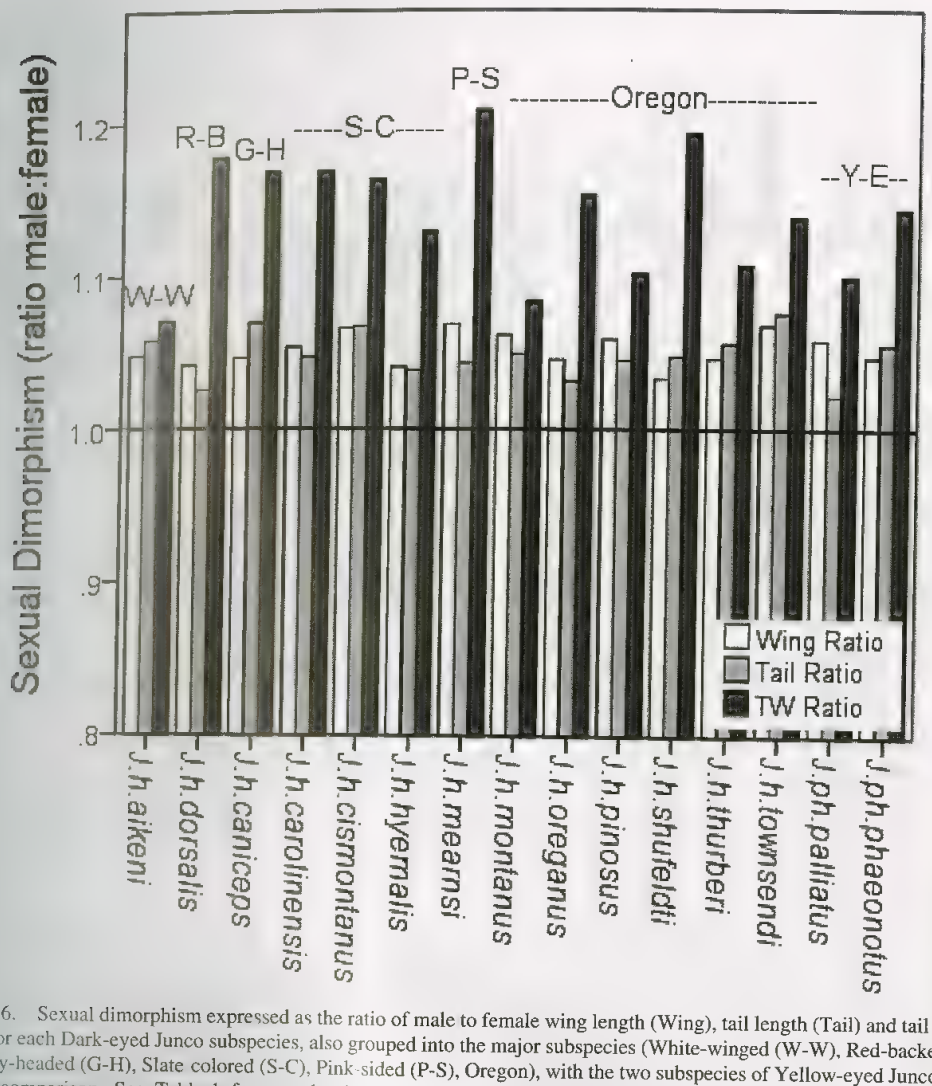


FIG. 6. Sexual dimorphism expressed as the ratio of male to female wing length (Wing), tail length (Tail) and tail white (TW) for each Dark-eyed Junco subspecies, also grouped into the major subspecies (White-winged (W-W), Red-backed (R-B), Gray-headed (G-H), Slate colored (S-C), Pink-sided (P-S), Oregon), with the two subspecies of Yellow-eyed Juncos (Y-E) for comparison. See Table 1 for sample sizes. A one-to-one ratio of male to female values is indicated by the horizontal line.

Across individuals of all subspecies, measures of body size (wing and tail length) were strongly correlated as were body size and tail white (Fig. 4). In general, subspecies with longer wings had longer tails, and those with larger wings and tails had more tail white (*J. h. aikeni* being the largest with the most tail white and *J. h. pinosus* being the smallest with least white). Alternatively, wing length, tail length, and tail white were not always correlated among individuals within each subspecies (Table 2). The most common correlation was between wing and tail length, seen among males in 10 of the 13 subspecies. There are many potential reasons for this correlation (Endler 1995). The traits may be genetically correlated based on shared mechanisms of growth, or correlational selection in relation to intra-sexual dominance interactions could favor males that are larger in both wing and tail length. Viability selection in relation to migration could also influence the correlation, but normally migration distance is positively related to wing length but favors a smaller tail to wing ratio (Fiedler 2005, Förschler and Bairlein 2011).

A hypothesis related to sexual selection for both longer wing and tail lengths in males is at

least partly supported by the fact that the correlation between wing and tail length was less common in females. The two traits positively covaried in females in only five subspecies, versus 10 subspecies in males. Fewer significant correlations among females than males could also in part be because of differences in sample size. Sometimes even with a correlation coefficient greater than that for males, the correlation for females was not significant. In the instances where female wing and tail length were correlated, it could be that viability or fecundity selection favors females of larger size in some populations but not others (Price and Liou 1989). In *J. h. carolinensis*, females with longer tails had higher fecundity (McGlothlin et al. 2005), one example of how larger size could relate to female reproductive output. For example, the intensity of fecundity selection could increase at higher latitudes or elevations where breeding seasons are short (Cox et al. 2003). Selection may also be stronger in some populations than others for females to compete with males for food, with dominance influenced by body size.

I also examined the correlation between body size and tail white within each subspecies, which was significant in only *J. h. aikeni* males. I expected to find this relationship in *J. h. carolinensis,* since it is in this subspecies that evidence for correlational selection on these traits currently exists (McGlothlin et al. 2005). Not accounting for the specimens' age upon capture could have made it difficult to detect trait correlations within subspecies if the relationships among the traits were not that strong and varied with age. Further, while evidence that wing length affects male dominance is widespread among the junco subspecies (*J. h. montanus,* Balph et al. 1979; *J. h. hyemalis,* Holberton et al. 1989; *J. h. hyemalis,* Ketterson et al. 1979; *J. h. pinosus,* EDF, unpubl. data), tail white may not influence mate attraction in many subspecies, and hence not correlate with body size. For example, in a population of *J. h. thurberi*, tail white recently evolved independently of wing length and does not relate to male breeding success (Price et al. 2008). Further studies can be used to examine the relative influence of tail white and wing length on male success within subspecies and whether variation in the function of these traits could help drive population divergence.

Finally, I determined how much the body size or tail white of individual subspecies deviated from the predicted values given the relationship between pairs of traits. The most striking patterns were first, that both male and female *J. h. aikeni* had significantly more tail white than expected given their body size (wing and tail length; Fig. 5). Individuals of this subspecies are overall the largest of the junco complex, but they still have more tail white than predicted based on the relationship between body size and tail white among subspecies. This supports the possibility that selection favors bright tails in *J. h. aikeni*, in addition to the fact that in only this subspecies were tail white and body size correlated. The pattern was possibly seen in both males and females because of their shared genetic background.

The other pattern worth noting was that the male and female Red-backed Juncos, *J. h. dorsalis,* had significantly longer tails than predicted from their wing lengths and less tail white than predicted from their body size (Fig. 5). The first question is why they have such long tails relative to their wings; their tail lengths are similar to those of the largest subspecies, *J. h. aikeni*, even though their wings are shorter. Given their large size, individuals of *J. h. dorsalis* also have relatively dull tails. In its body plumage and bill coloration *J. h. dorsalis* represents a sort of intermediate step between the ancestral Yellow-eyed Junco *J. h. phaenotous* and the other Dark-eyed Junco descendents (Milá et al. 2007). The residuals for the two Yellow-eyed Junco subspecies most closely resemble those of *J. h. dorsalis,* supporting the possibility that gene flow occurs between Yellow-eyed Juncos and *J. h. dorsalis* or that conditions are similar enough between their ranges to favor similar trait expression.

Sexual Dimorphism.—The final set of analyses involved comparing the magnitude of sexual dimorphism in wing length, tail length, and tail white among the subspecies. In most organisms where sexual selection acts, males are larger than females, and as predicted, males had longer wings and longer tails than females in all of the subspecies (Fig. 6). A comparison based on migration patterns could be helpful in explaining slight variations in the degree of dimorphism, since viability selection could favor more similar wing lengths in males and females in migratory subspecies compared to non-migratory subspecies, whereas sexual selection may select for longer wings in males but not in females (Mulvihill and Chandler 1990, Atwell et al. 2011). This

suggests that sexual dimorphism in wing length could be maintained via sexual selection even under viability selection on wing length.

Males also had whiter tails than females, with about 14% more tail white. The fact that tail white was more dimorphic than measures of body size supports the idea that it is a sexually selected trait (Hill et al. 1999, McGlothlin et al. 2005). In other words, there could be potentially strong sexual selection for white tails in males but not females. This difference could be related to testosterone, which is in higher concentrations in males than females, and at least in some junco subspecies is positively related to tail white (*J. h. carolinensis,* McGlothlin et al. 2008; *J. h. thurberi,* J.W. Atwell, pers. comm.). Alternatively, given their larger body size, males may have better access to food, which in turn leads to the development of more tail white in males than females (McGlothlin et al. 2007).

Tail white dimorphism was also more variable among the subspecies than wing or tail length dimorphism. This, again, could be related to geographic variation in the strength of sexual selection for tail white. For example, tail white is more sexually dimorphic in *J. h. carolinensis* where it is known to influence male reproductive success (Hill et al. 1999, McGlothlin et al. 2005) than in a population of *J. h. thurberi* where no such relationship has been found (tail white ratio male/female = 1.17 for *J. h. carolinensis*, Fig. 6, versus 1.14 for *J. h. thurberi,* calculated from Yeh 2004, Price et al. 2008). Geographic variation in the use of tail white as a signal could therefore help explain variation in the degree of sexual dimorphism in this trait.

Conclusions.—This study reveals variation in the mean, co-variation, and dimorphism of wing length, tail length, and tail white among the Dark-eyed Junco subspecies. While some of these observations have been made previously (Miller 1941), in no other study has tail white been quantitatively reported or examined in relation to proxies for body size. I found that tail white was much more variable across the subspecies than wing or tail length, suggesting that the strength of selection on tail white may vary geographically among the subspecies. In particular, *J. h. aikeni* stood out as having almost twice as much white on the tail feathers as the other subspecies. When considering how the traits co-varied, *J. h. aikeni* individuals had more tail white than expected even given their large body size. On the other hand, *J. h. dorsalis* individuals had longer tails and less tail white than expected for their size, patterns similar to those seen in the nearby and ancestral Yellow-eyed Juncos. Finally, the fact that tail white was the most sexually dimorphic trait, in addition to the most variable, further indicates a role for sexual selection in shaping its expression.

Is there any evidence that speciation is occurring within the Dark-eyed Junco species complex? In the early 1900s, when the specimens measured here were acquired, most subspecies hybridized at their contact zones (Miller 1941, Nolan et al. 2002). More recent observations suggest less fluidity between the subspecies. For example, *J. h. caniceps* (Gray-headed Juncos) and *J. h. thurberi* (Oregon Juncos) have overlapping breeding ranges in the Grapevine Mountains, Nevada. They do not appear to currently interbreed (Johnson and Cicero 2004), even though these two groups hybridized at this location in the past (Miller 1941). In another historical hybrid zone *J. h. carolinensis* individuals are dominant to *J. h. hyemalis*, both Slate-colored Juncos, even when controlling for body size (Wiedenmann and Rabenold 1987). In this example, dominance interactions could strengthen assortative mating and therefore further divergence.

In this study I cannot determine the relative roles of stochasticity, environmental or social conditions in creating the observed morphological variations among the Dark-eyed Junco subspecies. Although I discuss my observations primarily in relation to selection, chance likely also helped to shape the traits observed in these subspecies during their radiation (Milá et al. 2007). For example, drift, a founder effect, or a bottleneck can create a population in which the frequency distributions of continuous variables, like wing length or tail white, differ from the original population. At the same time, populations can have an underlying level of plasticity that produces phenotypic changes under new conditions; if these conditions then remain unchanged, such plasticity could eventually be lost and the new phenotypes become genetically fixed (Pigliucci et al. 2006). Furthermore, although I found some degree of variation in the traits I examined, in many ways the junco subspecies were similar. These similarities may reflect the common niche that juncos fill across their range or their relatively recent shared ancestry. Finally, other traits could be more influential in the subspecies' maintenance or further divergence (see Milá et al.

2007 for discussion of iris and beak coloration). For example, the White-winged Junco, *J. h. aikeni*, is so named for bright white wing bars not seen in the other subspecies (Sibley 2000). Further work can continue to identify the forces that shape the evolution of body size and tail white within each subspecies, and also the implications of the observed variation for interactions and divergence between them.

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MORPHOMETRIC MEASUREMENTS PERMIT ACCURATE SEXING OF THREE SPECIES OF MESOAMERICAN GROUND-SPARROW (GENUS: *MELOZONE*)

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ABSTRACT.—The natural history of many tropical bird species is poorly described, preventing more detailed studies of ecology, behavior, and evolution. For most sexually monochromatic tropical bird species, we lack field methodologies to categorize the sex of adults. In this study, we describe sex-based morphological differences of three monochromatic species in the genus *Melozone*: White-eared Ground-Sparrow, *M. leucotis*; Prevost's Ground-Sparrow, *M. biarcuata*; and Rusty-crowned Ground-Sparrow, *M. kieneri*. We collected six standard morphological measurements (tarsus length, tail length, wing chord length, culmen length, beak width, and beak depth) from live birds and museum specimens. We collected data from all recognized subspecies of the three Mesoamerican *Melozone* species. Morphological measurements capably distinguished males from females in all three species. In all cases, three or fewer morphological measurements were required to identify sex with accuracy levels that ranged from 75–100%, well beyond the 50% expected by chance. Comparisons involving all six measurements yielded accuracies that ranged from 58–93%. Our results provide the first field-based method for estimating the sex of individuals in this poorly studied genus of tropical birds. We recommend our findings be used to distinguish males from females in banding stations where *Melozone* ground-sparrow species occur. *Received 11 November 2012. Accepted 4 April 2013.*

Key words: dimorphism, Emberizidae, *Melozone biarcuata*, *Melozone kieneri*, *Melozone leucotis*, morphometric differences, sex discrimination.

Approximately 70% of bird species inhabit the tropics (BirdLife International 2012), but basic natural history, demography, breeding and molting information is lacking for many tropical bird species (Ricklefs and Wikelski 2002, Martin 2004, Ryder and Wolfe 2009, Sandoval and Barrantes 2009, Wolfe et al. 2010). In North America and Europe, documented morphological differences between males and females allow for more advanced ornithological research (e.g., Baker 1992, Pyle 1997, Marquiss and Rae 2002, Cuthbert et al. 2003, Jensen et al. 2003). The lack of information pertaining to tropical bird natural history precludes studying the more detailed aspects of the birds' ecology, behavior, and reproduction.

Many investigations rely on accurate classification of the sex and age of individual birds (Pérez-Tris et al. 1999, Bensch et al. 2002). Discrimination between the sexes remains a challenge, however, in species where males and females share similar plumage and behavior (e.g., Donohue and Dufty 2006, Tórrez and Arendt 2012). One relatively recent technique for sexing birds is the use of molecular markers (Griffiths et al. 1998, Fridolfsson and Ellegren 1999, Waits and Paetkau 2005), but the application of this technique is still limited by cost and restrictions on blood sampling (de la Hera et al. 2007). Therefore, traditional techniques for sexing birds, based on morphometric measurements, are both necessary and important (Martín et al. 2000, Radley et al. 2011).

Here, we present morphological data for identifying the sex of individuals in three monochromatic *Melozone* ground-sparrows that inhabit Mesoamerica: White-eared Ground-Sparrow (*M. leucotis*), Prevost's Ground-Sparrow (*M. biarcuata*), and Rusty-crowned Ground-Sparrow (*M. kieneri*). We base our comparisons on measurements collected from both live birds and museum specimens. We include data for all the described subspecies for each of the three species. Importantly, we include morphological data for two taxa of Prevost's Ground-Sparrows that may represent two unique species. This is the first detailed morphological analysis for sexing individuals in all three of these tropical ground-sparrows.

METHODS

Study Species.—The White-eared Ground-Sparrow inhabits the Pacific slope of Mexico from Chiapas to El Salvador, northern and central Nicaragua, and northeastern Costa Rica, from 450–2,000 m elevation (Stiles and Skutch 1989,

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Howell and Webb 1995). The Prevost's Ground-Sparrow inhabits the Pacific slope and interior of Chiapas to western Honduras and El Salvador, and the Central Valley of Costa Rica, from 250–2,000 m elevation (Stiles and Skutch 1989, Howell and Webb 1995). The Rusty-crowned Ground-Sparrow inhabits the Pacific slope of Mexico from south of Sonora and the interior from Jalisco to northwest Oaxaca, from 0–2,000 m elevation (Howell and Webb 1995). Throughout much of their distributions in Guatemala and Costa Rica, the ranges of White-eared and Prevost's ground-sparrows overlap; the Rusty-crowned Ground-Sparrow is allopatric with respect to the other two species (Howell and Webb 1995). All three species live in thicket habitats, young successional forest, and shade coffee plantations (Stiles and Skutch 1989, Howell and Webb 1995, Sandoval and Mennill 2012). These habitats—especially thicket habitats—are increasingly threatened from anthropogenic habitat modification and are afforded no special conservation protection (Sánchez et al. 2009, Biamonte et al. 2011). Consequently, the conservation of habitat for all three ground-sparrow species is of concern.

The taxonomy of the Prevost's Ground-Sparrow is controversial. The Costa Rican endemic subspecies *M. b. cabanisi* is quite different from the two more northerly subspecies (*M. b. biarcuata* and *M. b. hartwegi*), based on anecdotal observations of plumage and vocal differences (Stiles and Skutch 1989, Howell and Webb 1995, AOU 1998). Given that our ongoing studies suggests that *M. b. cabanisi* may be a distinct species (LS and DJM, unpubl. data), we conducted a single analysis of sex identification for *M. b. cabanisi*, and a second analysis for *M. b. biarcuata* and *M. b. hartwegi*.

Measurement Methods.—We obtained morphological measurements from two sources: live individuals measured in the field and museum specimens. In the field, we captured birds with mist nets and collected morphometric measurements during the breeding season. We distinguished females based on the presence of brood patches (only females are known to incubate in the genus *Melozone*), and we distinguished males on the basis of cloacal protuberances (Sandoval and Mennill 2012). We visited the following four museums to measure specimens: (1) Museo de Zoología Universidad de Costa Rica, San José, Costa Rica; (2) Museo Nacional de Costa Rica, San José, Costa Rica; (3) the Field Museum of Natural History, Chicago, U.S.A.; and (4) the University of Michigan Museum of Zoology, Ann Arbor, U.S.A. We measured both live birds and museum specimens for White-eared and Prevost's Ground-Sparrows (*M. b. cabanisi* subspecies). We collected all measurements from birds with definitive plumage (Stiles and Skutch 1989, Howell and Webb 1995). LS collected all measurements from both live birds and museum specimens.

We took six morphological measurements from each adult bird: tarsus length (from the intertarsal joint to the middle of the sole of the foot), tail length, wing chord length (unflattened), culmen length (from tip of the bill to the base of the skull), bill width (at bill gape), and bill depth (measured at a right angle at the point on the lower mandible where the feathers end). We used a dial caliper (model: SPI Plastic Caliper 150 mm, AVINET, NY, USA) to obtain the bill and tarsus measurements, and a metallic wing rule (model: WING-15ECON, AVINET, NY, USA) to measure the wing chord and tail length.

Statistical Analyses.—We conducted backward stepwise discriminant function analysis to examine morphological differences between males and females for each *Melozone* species. Some controversy exists concerning stepwise analysis. We compared the "best model" (the model with the lowest number of predictor variables and highest percentage of correct classification of sexes) against the model including all variables using Akaike Information Criterion (AIC; see Table 1). Given our small sample sizes for some species, we used the AIC corrected (AIC_c) formula to select the best model for separating sexes (Burnham et al. 2011). We considered models to be different when the AIC_c value between the two most competitive models was larger than two (Burnham et al. 2011). We also estimated model weight (AIC_w), which represents the amount of variation explained by each model (Burnham et al. 2011). We averaged the models based on the AIC_c weights if the model with all the variables and the "best model" were not different (Burnham et al. 2011). In all of our analyses, we report the percent of correct sex classification based on a cross-validation method using a jackknifed "leave-one-out" approach (Krebs 1999, Sandoval and Barrantes 2012).

We used a Student's *t*-test to compare differences between sexes in each morphological measurement selected by the "best model" in

TABLE 1. Comparisons between different models for distinguishing the sex of three Mesoamerican *Melozone* ground-sparrows using six morphological measurements, including models that use all measurements (i.e., the "whole model"), and the most competitive models with fewer predictor variables that facilitate improved sex classification. Bold type identifies the "best model" for each species, according to AIC_c values.

Model	Parameters	AIC_c	ΔAIC_c	AIC_w
White-eared (*M. leucotis*)				
Best model: Wing	**2**	**30.26**	**0**	**0.98**
Whole model	7	38.01	7.75	0.02
Prevost's (*M. b. biarcuata* and *hartwegi*)[a]				
Best model: Tail + Wing	**3**	**14.57**	**0**	**0.97**
Whole model	7	21.35	6.78	0.03
Prevost's (*M. b. cabanisi*)[a]				
Best model: Tarsus + Culmen + Bill depth	**4**	**15.93**	**0**	**0.99**
Whole model	7	25.59	9.66	0.01
Rusty-crowned (*M. kieneri*)				
Best model: Tarsus + Wing + Culmen	**4**	**21.26**	**0**	**0.99**
Whole model	7	29.71	8.45	0.01

[a] Owing to taxonomic controversy surrounding Prevost's Ground-Sparrows, we present results separately for the two recognized subspecies groups (see methods for details)

the discriminant analysis. We used SYSTAT (version 11.00.01; SYSTAT Software, Chicago, IL, USA) to conduct the statistical analyses.

RESULTS

Our analyses revealed substantial morphological differences between male and female ground-sparrows. In general, models that best distinguished male from female tropical *Melozone* ground-sparrows contained three or fewer morphological measurements (Table 1). Different combinations of morphometric measurements produced the best separation of males from females across the three species (Table 1).

White-eared Ground-Sparrow.—We analyzed 82 adult individuals (31 females and 51 males) of the three subspecies (71 *M. l. leucotis*, three *M. l. nigrior*, and eight *M. l. occipitalis*), including 60 live birds and 22 museum specimens. The model that included all morphological measurements (whole model: Wilk's $\lambda = 0.42$, $F_{6,75} = 17.51$, $P < 0.001$) classified correctly 90% of females and 86% of males. The "best model" included only wing length (Wilk's $\lambda = 0.44$, $F_{1,80} = 100.16$, $P < 0.001$) and classified correctly 94% of females and 88% of males. Males had longer wings than females ($t_{80} = -10.00$, $P < 0.001$, Table 2). The classification function for the best model was:

$$\text{Sex} = -34.68 + \text{Wing} * 0.44$$

Function values (mean ± SE) for females were −1.42 ± 0.18 and for males were 0.86 ± 0.18. For all morphometric measurements, males were larger than females (Table 2).

Given the large number of measured White-eared Ground-Sparrows, including live birds and specimens, we compared morphometric measurements between both sources. We found no differences in mean morphometric measurements from live birds versus museum specimens for five of the six measurements (Table 3). The only measurement that differed between live birds and specimens was tarsus length, which differed for both sexes (Table 3); tarsi were longer in live birds than in specimens. This difference did not affect our results for White-eared Ground-Sparrows, because tarsus was not selected in our "best model."

Prevost's Ground-Sparrow (M. b. biarcuata and M. b. hartwegi).—We analyzed 36 adult individuals (nine females and 27 males) of the two subspecies (31 *M. b. biarcuata* and 16 *M. b. hartwegi*), all from museum specimens. The model with all morphological measurements (whole model: Wilk's $\lambda = 0.33$, $F_{6,29} = 9.77$, $P < 0.001$) classified correctly 93% of females and 78% of males. The "best model" included tail and wing length (Wilk's $\lambda = 0.38$, $F_{2,33} = 21.21$, $P < 0.001$) and classified correctly 93% of females and 89% of males. Males had longer tails ($t_{34} = -5.15$, $P < 0.001$, Table 2) and longer wings ($t_{34} = -10.00$, $P < 0.001$, Table 2). The classification function was:

$$\text{Sex} = -34.23 + \text{Tail} * 0.19 + \text{Wing} * 0.32$$

TABLE 2. Differences between six morphological measurements of three Mesoamerican *Melozone* ground-sparrow species by sex. Bold type identifies measurements selected in the best model to distinguish sex in each species. Shown are the upper and lower confidence intervals (CI) at 95% accuracy of the full range of data for each sex.

	Female			Male		
	Lower CI	Mean	Upper CI	Lower CI	Mean	Upper CI
White-eared Ground-Sparrow						
Tarsus	24.85	27.90	30.95	26.69	29.12	31.55
Tail	60.66	68.94	77.22	65.27	72.57	79.87
Wing	**71.80**	**76.36**	**80.92**	**77.11**	**81.59**	**86.07**
Culmen	12.83	14.18	15.53	13.14	14.48	15.82
Bill width	8.52	9.56	10.60	8.62	9.90	11.18
Bill depth	7.76	8.56	9.36	9.37	10.33	11.29
Prevost's Ground-Sparrow (*M. b. biarcuata* and *M. b. hartwegi*)[a]						
Tarsus	22.92	24.10	25.28	23.09	25.00	26.91
Tail	**56.21**	**60.78**	**65.35**	**60.28**	**66.67**	**73.06**
Wing	**58.70**	**63.99**	**69.28**	**65.16**	**69.48**	**73.80**
Culmen	11.53	12.92	14.31	12.08	13.25	14.42
Bill width	6.77	8.04	9.31	6.92	8.14	9.36
Bill depth	7.15	8.16	9.17	7.64	8.56	9.48
Prevost's Ground-Sparrow (*M. b. cabanisi*)[a]						
Tarsus	**22.34**	**24.10**	**25.86**	**21.75**	**23.85**	**25.95**
Tail	49.36	56.00	62.64	54.04	59.71	65.38
Wing	62.59	67.32	72.05	62.29	68.68	75.07
Culmen	**11.45**	**12.06**	**12.67**	**11.81**	**12.59**	**13.37**
Bill width	7.29	8.30	9.31	7.40	8.42	9.44
Bill depth	**6.91**	**7.76**	**8.61**	**7.20**	**8.21**	**9.22**
Rusty-crowned Ground-Sparrow						
Tarsus	**21.93**	**24.02**	**26.11**	**23.00**	**24.96**	**26.92**
Tail	57.98	68.33	78.68	64.05	71.08	78.11
Wing	**65.62**	**72.32**	**79.02**	**70.14**	**75.62**	**81.10**
Culmen	**11.86**	**13.05**	**14.24**	**12.38**	**13.51**	**14.64**
Bill width	7.38	8.22	9.06	7.16	8.42	9.68
Bill depth	7.40	8.31	9.22	7.64	8.37	9.10

[a] Owing to taxonomic controversy surrounding Prevost's Ground-Sparrows, we present results separately for the two recognized subspecies groups (see methods for details).

Function values for females were −2.16 ± 0.37 and for males were 0.72 ± 0.18. For all morphometric measurements, males were larger than female (Table 2).

Prevost's Ground-Sparrow (M. b. cabanisi).—We analyzed 20 adult individuals (five females and 15 males), including two live birds and 18 museum specimens. The model with all morphological measurements (whole model: Wilk's $\lambda = 0.31$, $F_{6,12} = 4.49$, $P = 0.01$) classified correctly 80% of females and 71% of males. The "best model" included tarsus length, culmen, and beak depth (Wilk's $\lambda = 0.46$, $F_{3,15} = 5.93$, $P = 0.007$); this model classified correctly 100% of females and 86% of males. Males had longer culmens than females ($t_{18} = 3.11$, $P = 0.006$, Table 2), whereas their tarsus length ($t_{18} = -0.033$, $P = 0.97$, Table 2) and bill depth ($t_{18} = -1.75$, $P = 0.10$, Table 2) did not significantly vary in pair-wise comparisons. The classification function was:

$$\text{Sex} = -27.82 - \text{Tarsus} * 0.778 + \text{Culmen} * 2.66 + \text{Bill depth} * 1.642$$

Function values for females were −1.72 ± 0.14 and for males were 0.62 ± 0.30. For all morphometric measurements, males were larger than females (Table 2).

Rusty-crowned Ground-Sparrow.—We analyzed a total of 32 adult individuals (12 females and 20 males) of the three subspecies (29 *M. k. kieneri*, one *M. k. grisior*, and two *M. k. rubricatum*), all from museum specimens. The model with all morphological measurements (whole model: Wilk's

TABLE 3. Morphometric differences between live birds and museum skins based on sex in White-eared Ground-Sparrows (*Melozone leucotis*). Values are shown as mean ± SE.

	Male				Female			
	Live	Museum	t_{49}	P	Live	Museum	t_{29}	P
Tarsus	27.77 ± 0.90	27.39 ± 0.21	12.00	<0.001	28.56 ± 0.20	26.01 ± 0.52	−5.56	<0.001
Tail	72.68 ± 0.43	72.29 ± 1.56	0.33	1	68.52 ± 0.72	70.12 ± 2.16	−0.92	1
Wing	82.00 ± 0.33	80.52 ± 0.73	2.12	0.23	73.44 ± 0.52	76.15 ± 0.58	0.30	1
Culmen	14.46 ± 0.11	14.54 ± 0.19	−0.37	1	14.17 ± 0.15	14.21 ± 0.24	−0.13	1
Bill width	10.00 ± 0.07	9.61 ± 0.27	1.99	0.31	9.65 ± 0.10	9.29 ± 0.23	1.73	0.56
Bill depth	10.88 ± 2.20	8.87 ± 0.20	0.56	1	8.52 ± 0.08	8.67 ± 0.18	−0.94	1

$\lambda = 0.51$, $F_{6,25} = 3.99$, $P = 0.006$) classified correctly 58% of females and 70% of males. The "best model" included tarsus, wing, and culmen length (Wilk's $\lambda = 0.52$, $F_{3,28} = 8.77$, $P = 0.003$); this model classified correctly 75% of females and 85% of males. Males had longer tarsi ($t_{30} = -2.78$, $P = 0.009$, Table 2), wings ($t_{30} = -10.00$, $P < 0.001$, Table 2), and culmens than females ($t_{30} = -2.00$, $P = 0.05$, Table 2). The classification function was:

$$\text{Sex} = -33.556 + \text{Tarsus} * 0.403 + \text{Wing} * 0.839 + \text{Culmen} * 0.443$$

Function values for females were −1.21 ± 0.31 and for males were 0.73 ± 0.21. For all morphometric measurements, males were larger than females (Table 2).

DISCUSSION

Morphometric measurements provided an efficient tool for estimating the sex of definitive plumage birds in three Neotropical ground-sparrows in the genus *Melozone*: White-eared, Prevost's, and Rusty-crowned ground-sparrows. In all cases, three or fewer morphometric measurements facilitated sex identification with accuracy levels ranging from 75–100%. It is noteworthy that there were varying degrees of overlap in males and females for each of the six morphometric measurements, contributing to errors in classification accuracy; female White-eared and Prevost's ground-sparrows presented higher classification accuracy than males; whereas, male Rusty-crowned Ground-Sparrows were more consistently classified to the correct sex than females.

Across all of the study species where we evaluated sexual size dimorphism, males were consistently larger than females. A similar pattern of size dimorphism is known from three North American *Melozone* species (Abert's Towhee, *M. aberti*: Tweit and Finch 1994; Canyon Towhee, *M. fuscus*: Johnson and Haight 1996; and California Towhee, *M. crissalis*: Benedict et al. 2011), where males showed significantly larger tarsus, wing, and beak measurements in comparison to females. In our analyses, wing length was the most consistently informative sex discrimination measurement and was included in the "best model" in three of our four analyses. Tarsus and culmen measurements were included twice in the "best models."

In all three species that we studied, we observed substantial overlap between male and female measurements. These data points underscore the importance of corroborating the sex of measured birds using presence of incubation patch and clocal protuberances during the breeding season. Both characteristics appear to be exclusive to females or males, respectively, in these species (Sandoval and Mennill 2012; LS and DJM, unpubl. data).

We provide discriminant formulas that can be used by researchers at banding stations to differentiate males from females, even at times of year when other indicators such as brood patches and cloacal protuberances are absent. The ability to differentiate sex in these three Neotropical ground-sparrow species will be valuable in future investigations of this group, particularly given that all of the species exhibit sexually monomorphic plumage. For example, sex identification will help conduct population analyses to evaluate the demographic consequences of habitat changes; all three species are specialists in thickets, secondary forest edges, and shade coffee plantations (Stiles and Skutch 1989, Howell and Webb 1995, Sandoval and Mennill 2012) and these habitats have little protection throughout their respective ranges. Research in these habitats can inform effective management and conservation plans,

which are important for many other resident and migratory bird species (Clergeau et al. 1998, Crooks et al. 2004, Donnelly and Marzluff 2004, Chace and Walsh 2006, Biamonte et al. 2011) as well as other animals (Andrén 1994, Fahrig 2003, Angold et al. 2006).

The reasons for sexual size dimorphism in songbirds are not well understood (Badyaev and Hill 1999). Multiple explanations for sexual size dimorphism in Neotropical ground-sparrows are possible. (1) Larger male body size may be promoted if females prefer to mate with larger males, because they produce lower-frequency songs that are more attractive to females, as in other species of songbird (Wallschläger 1980, Baptista 1996). (2) Larger body size may confer on males a competitive advantage when defending breeding territories against rivals, driving larger body sizes for males. These possible explanations need further research.

Comparisons between live birds and museum specimens in White-eared Ground-Sparrows showed no significant differences in five of the six standard morphometric measurements that we used. Tarsus measurements were smaller in specimens than in live birds, for both males and females, probably because soft tissue shrinks over time (Greenwood 1979, Harris 1980, Bjordal 1983, Winker 1993). Contrary to several studies (West et al. 1968, Green 1980, Engelmaer et al. 1983, Jenni and Winkler 1989), we found that wing and tail length, and bill measurements were similar between live birds and specimens.

In conclusion, our results provide a field-based method for differentiating the sex of individuals in three species of *Melozone* ground-sparrow. We recommend that our results be used as a tool by other ornithologists, including those at banding stations where *Melozone* ground-sparrows occur. We encourage bird banders throughout the tropics to collect molt information and morphometric measurements that facilitate sex differentiation and age categorization of captured individuals.

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DEMOGRAPHIC COMPARISON OF GOLDEN-WINGED WARBLER (*VERMIVORA CHRYSOPTERA*) POPULATIONS IN NORTHERN AND SOUTHERN EXTREMES OF THEIR BREEDING RANGE

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ABSTRACT.—Conservation strategies for declining species often are based on limited knowledge about how fecundity and survival may change across a species' range, and what factors may be limiting for a given population. Incomplete understanding of how a species' demography varies across a range of conditions may lead to inappropriate management decisions. Our objective was to compare demographic data from northern and southern extremes of the breeding range of Golden-winged Warblers (*Vermivora chrysoptera*). Specifically, we compared minimum estimates of annual adult survival, daily nest survival, fecundity, and population growth (lambda) for Tennessee and Ontario breeding populations. Tennessee nest survival decreased throughout the nesting season and as daily minimum temperature increased, but the constant survival model was equally supported (model averaged daily survival rate, DSR = 0.972 [0.01 SE]). Ontario nest survival also decreased throughout the nesting season, but not as a function of temperature (model averaged DSR = 0.956 [0.02 SE]). Despite larger clutch sizes and number of young fledged per successful nest in Ontario, fecundity estimates were greater for the Tennessee population. Males had greater annual survival than females in both Tennessee and Ontario populations (Tennessee male = 0.616 [0.11 SE], Tennessee female = 0.427 [0.12 SE], Ontario male = 0.618 [0.08 SE], and Ontario female = 0.477 [0.14 SE]). Minimum lambda estimates suggest that both populations were declining (λ = 0.7468 and 0.7935 for Tennessee and Ontario, respectively). However, as with many mark-recapture studies of birds, we are unable to separate mortality from dispersal which likely biases these survival estimates. Further, annual survival is affected by events in the wintering and migratory periods and until these are known, we will be limited in our ability to effectively manage this and other declining Neotropical migratory songbirds. *Received 24 September 2012. Accepted 22 April 2013.*

Key words: annual adult survival, daily nest survival, geographic variation, life history, Neotropical migratory songbird, warbler.

INTRODUCTION

Geographic variation in species life history traits has been a phenomenon of interest in ecology for decades. Most well documented in birds is the trend for increased clutch sizes at higher latitudes (Lack 1947, Cody 1966). Many of the hypotheses explaining latitudinal differences in clutch size (i.e., nest predation, food availability, and season length) may also apply to other life history parameters such as adult survival, nest survival, and annual fecundity. Recent studies of avian life history variation include such parameters (Mattsson et al. 2011, Wilson and Martin 2011) and, as a result, further our understanding of both the focal species and life history theory in general. Such studies demonstrate that to achieve the greatest fitness, organisms must balance tradeoffs between reproduction and survival (Stearns 1989, Ricklefs 2000). Further, if selection pressures vary geographically (as they often do), then organisms in different regions may rely on different strategies (Morrison and Hero 2003, Ardia 2005, McNamara et al. 2008, Mattsson et al. 2011).

In addition to contributing to theory, an understanding of geographic variation in demography can provide a framework within which to focus conservation efforts for declining species. Many Nearctic-Neotropical migrant songbirds experiencing population declines have large breeding ranges that extend from the southeastern United States into southeastern Canada. Although the causes of such declines may vary geographically, conservation efforts are often applied uniformly, range-wide. For these widely-distributed species, comparisons of demographics and limiting factors across the range provide an important basis for effective conservation. For example, if northern populations are limited more by adult survival and southern populations more by fecundity, conservation efforts would best be applied on a region-specific basis. There is a real

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need for more species-specific geographic comparisons of demographic rates to aid in developing theory and applying conservation efforts. Such efforts for declining and wide ranging species are often as simple as integrating the findings from ongoing studies or using historical datasets from other regions for comparison (e.g., Wilson and Martin 2011).

The Golden-winged Warbler (*Vermivora chrysoptera*) is a Nearctic-Neotropical migratory, ground-nesting songbird that uses early successional habitats for breeding (Confer et al. 2011) and is experiencing population declines throughout its breeding range (-2.6/year since 1966, Sauer et al. 2011) from the southern Appalachians to southern Canada. Causes of decline are likely related primarily to two factors: (1) hybridization and competition with Blue-winged Warblers (*V. cyanoptera*: Gill 1997; Vallender et al. 2007a, b, 2009) and (2) habitat loss (on both breeding and wintering grounds) associated with maturing forests and human development (Buehler et al. 2007, Confer et al. 2011). Despite our understanding of these two primary causes of decline, it is not known if there are more specific population limiting factors that may vary geographically such as survival and reproductive success. To assess this we compared two multi-year demographic datasets for the Golden-winged Warbler; one from the Cumberland Mountains of Tennessee (36° latitude) and the other from the Canadian Shield of southern Ontario (44° latitude), separated by approximately 1,000 km. Specifically, we compared estimates of minimum annual adult survival, daily nest survival, and lambda (the finite rate of population growth) for both populations. We expected that the northern population in Ontario would have greater fecundity than the population in Tennessee based on hypotheses of increased predation (Skutch 1949, Martin 1995) and smaller clutch sizes at southern latitudes (Ashmole 1963). This species is single-brooded, and variance in fecundity will be caused by differences in the number of young fledged and daily nest survival rates.

METHODS

Study Area - Tennessee

The Cumberland Mountains in Tennessee are located near the southern extreme of the breeding range of Golden-winged Warblers. The mean elevation is 580 m and the highest ridges reach 1,075 m. The predominant landcover of the region is mixed-mesophytic forest, and approximately 15% is in early stages of succession because of the surface mining of coal and timber harvests (LB and DB, unpubl. data). In this region, Golden-winged Warblers occupy reclaimed and abandoned surface mines and sites after timber harvests until the herbaceous vegetation is lost following succession.

Our study sites are located within the Northern Cumberlands Wildlife Management Area on four reclaimed coal surface mines (40–120 ha); two were reclaimed ~15 years before the study and the other two were reclaimed ~20–25 years before the study. Mine reclamation on these sites typically involved planting a thick herbaceous layer of grasses and forbs (to prevent soil erosion) and black locust (*Robinia pseudoacacia*) saplings. Since reclamation, maples (*Acer* spp.), yellow poplar (*Liriodendron tulipifera*), oak (*Quercus* spp.), and thickets of blackberry (*Rubus* spp.) have become established. Periodic fires (historically, arson and natural, and more recently, managed) have maintained the thick herbaceous cover and created numerous snags in all sites. All study sites were at approximately the same elevation (mean = 850 m, range = 770–950 m). We selected these sites based on the relatively high concentration of breeding golden-winged pairs to efficiently focus our nest searching and monitoring efforts.

Study Area - Ontario

All study sites in Ontario were in the area surrounding the Queen's University Biological Station (QUBS), near Chaffey's Lock, Ontario, Canada, with a total area of ~2,000 ha with ~500 ha in early successional habitat suitable for Golden-winged Warblers. This landscape was a patchy matrix of mature closed-canopy second-growth deciduous forest, interspersed with active and abandoned agricultural fields in varying stages of succession (~10–15% of the landscape) along with numerous small lakes and swamps. The area is primarily comprised of rolling terrain with ridges of granite outcrops alternating with valleys every ~500 m (mean elevation ~125 m). Most openings in the forest resulted from past anthropogenic land clearing (mid-late 1800s); however, natural clearings created by exposed bedrock outcrops and beaver ponds were also common. Species first colonizing abandoned fields and clearings in the area include common

prickly ash (*Zanthoxylum americanum*), American elm (*Ulmus americana*), American hornbeam (*Carpinus caroliniana*), gray dogwood (*Cornus racemosa*) and American red raspberry (*Rubus idaeus*). Study sites occupied by Golden-winged Warblers were chosen opportunistically throughout this landscape matrix—dictated by the patchy distribution of the suitable habitat—and were primarily clustered in areas near accessible roads. These clusters of Golden-winged Warblers typically contained between 5–10 breeding pairs, but some isolated pairs were also included. In general, sites with clusters of breeding pairs were chosen in both regions to increase our sample of nesting attempts in this cryptic species.

Field Methods

From 20 April to 30 June 2003–2006 in Tennessee and from 1 May to 15 July 2003–2006 in Ontario, we visited each site every 2–3 days from sunrise (~0600 hrs) to mid afternoon. To locate nests of Golden-winged Warblers, we carefully observed behavior, especially during nest building and nestling periods when visits to the nests were frequent. In both Tennessee and Ontario, we found the majority of nests (~70% in both locations) during the nest-building stage. We monitored all nests every 2–4 days until the nestlings fledged or the nest failed. After nest failures (eggs or nestlings missing before nestling age day 9), we attempted to find evidence of re-nesting. We were able to find some re-nesting activity and only one case of a second re-nesting attempt after two predation events. There was no evidence of nest parasitism of Golden-winged Warblers by Brown-headed Cowbirds (*Molothrus ater*) in the Tennessee population and only low rates in Ontario (three nests each containing one cowbird egg across the 4 years).

We banded and color-marked adult male and female Golden-winged Warblers to allow for individual identification. To capture and band adult males, we placed a male decoy in a small tree or shrub near a mist net and played a golden-winged song to elicit an aggressive response. To capture adult females, we flushed them into a mist net placed near the nest while the female was incubating eggs or, less commonly, while brooding young. We did not attempt to flush females from the nest until after at least 6 days of incubation to prevent nest abandonment. No females abandoned their nests as a result of this disturbance. We aged all individuals as SY, AHY or ASY using plumage criteria described in Pyle (1997). Color-marked adult male and female Golden-winged Warblers were re-sighted in consecutive years during nest searching and systematic surveys of all sites. Nestlings in the study area in Tennessee were also banded on ~day 4–5 with an aluminum band and a single year cohort color to enable us to identify second year individuals returning to breed.

Data Analyses

Nest Survival.—We tested whether daily nest survival rates were different for the Ontario and Tennessee populations by combining the two datasets and modeling the effects of region, year, and time throughout the nesting season (linear time trend model). We then modeled the relationship between daily nest survival rate (DSR) and variables based on *a priori* hypotheses (see below) for each population separately to obtain estimates of daily nest survival to use in regional calculations of fecundity. For each population we used Akaike's Information Criterion (AIC_c) adjusted for small sample size for model selection (Burnham and Anderson 2002) in all analyses. We modeled daily nest survival as a function of year, daily precipitation, minimum daily temperature, time of season (both linear and quadratic models), nestling age, nest stage, a global model containing all variables, and a null model containing the intercept only (i.e., constant survival).

We expected annual variation in nest survival because of changes in regional weather patterns and/or annual fluctuations in predator abundance. For the Tennessee population, we had sufficient sample sizes to model nest survival in 2004–2006; for the Ontario population, we had sufficient data for 2003–2006. We hypothesized that temperature and/or precipitation could impact daily nest survival rate by influencing female incubating and brooding behavior, as has been demonstrated in previous studies for other species (Siikamäki 1996, Radford et al. 2001). We obtained temperature and precipitation data from the National Oceanic and Atmospheric Association (NOAA) Climatic Data Center (station # 723246 KOQT Oak Ridge) for Tennessee and directly from a weather station located at QUBS for Ontario.

We used Program MARK (White and Burnham 1999, Rotella et al. 2004) to run the nest survival models and to obtain estimates of daily nest survival for both populations. We assumed a 25-day nesting cycle for Golden-winged Warblers

with 4 days for laying, 11 days for incubation and 10 days for nestlings (Confer et al. 2011). As suggested by Dinsmore et al. (2002), we did not standardize individual covariates.

Adult Survival.—We tested whether annual adult survival rate (Φ) and recapture/re-sighting probabilities (p) were different for the Ontario and Tennessee populations by combining the two datasets and modeling the effects of region, year, and sex with the Cormack-Jolly-Seber (CJS) model (Pollock et al. 1990, Lebreton et al. 1992) using Program MARK (White and Burnham 1999). We then modeled survival of adult Golden-winged Warblers and recapture/re-sighting probabilities separately for each population to obtain annual survival estimates for each. We chose the set of candidate models *a priori* based on our knowledge of the species and the limitations of our data. For example, we were unable to assess differences in survival between hatch-year and after hatch-year birds because too few individuals returned as second-year birds after being banded as nestlings in the previous breeding season (<10% in Tennessee and Ontario despite marking >100 nestlings/year). Likewise, we could not test for differences in survival between hybrids and phenotypically pure birds, because hybrids were relatively rare in both banded populations. Phenotypic hybrids comprised <10% of the Tennessee population and ~30% in the Ontario population during our study years, although genetic analyses have indicated that cryptic hybrids (i.e., phenotypic Golden-winged Warblers with Blue-winged Warbler-specific mitochondrial DNA) exist in both populations (Vallender et al. 2007b, 2009).

We modeled Φ and p as a function of sex, year, and sex*year interactions for both Tennessee and Ontario populations. Differences in annual male and female survival were expected because of weather events or annual fluctuations in food availability on the breeding and/or non-breeding grounds as well as during migration. Ideally, there were no differences in re-sighting probability among years indicating consistent field crew effort and no annual changes in bird behavior. However, differences in re-sighting probability were expected between males and females because of the inconspicuous behaviors associated with breeding females compared with males. To obtain final point estimates (and standard errors) for Φ and p, we used model averaging (Burnham and Anderson 2002) in Program MARK. To determine if there was significant over-dispersion, we assessed model goodness of fit for our most parameterized model for each population using the median c-hat approach in Program MARK. Median c-hat estimates for the Ontario and Tennessee populations were 1.07 and 0.98, respectively, which suggested good model fit (Lebreton et al. 1992).

Lambda Estimation.—We used the model-averaged estimates for adult female survival and daily nest survival rates to develop a single sex, two-stage Leslie population projection matrix. We assumed hatch-year female survival (from fledging to first year breeding) to be half of after hatch-year female survival (Temple and Cary 1988, Donovan et al. 1995). We used PopTools (Hood 2010) to estimate lambda (λ), the finite rate of population growth, for both the Tennessee and Ontario populations. To calculate fecundity, we used the following equation:

$$F = \text{mean number of young fledged} \times \text{sex ratio} \times \left(2p - p^2\right)$$

where the sex ratio is assumed to be 0.5 and p is the apparent nest success rate (DSR^{25} where 25 is the number of days in the nesting cycle). The $2p - p^2$ term accounts for one re-nesting attempt after a failed nest (Giocomo 2005, Buehler et al. 2008), which occurs regularly in golden-wingeds in both Tennessee and Ontario (LB and RV, pers. obs.). This assumes that re-nesting rates are 100%, and therefore likely biases our estimates of fecundity to be high. While we observed one instance of a second re-nest, we did not include a parameter for more than one re-nesting attempt because we felt our fecundity estimates were already biased somewhat high. We compared elasticity values for survival and reproduction in young (SY) and mature (ASY) females. Elasticity values measure proportional sensitivity of λ to changes in demographic parameters, specifically the incremental proportional rate of change in λ as a result of incremental proportional rate of change in a demographic parameter (Caswell 2001).

RESULTS

For the Tennessee population, we monitored 102 nests of Golden-winged Warblers during the 2004–2006 breeding seasons for a total of 1,613 exposure days across a 55-day nesting season. For the Ontario population, we monitored 86 nests of Golden-winged Warblers during the 2003–2006

TABLE 1. Summary of demographic information for populations of Golden-winged Warblers (*Vermivora chrysoptera*) in Tennessee and Ontario derived from field data and from analyses. Data were used to develop a two stage Leslie Matrix. All values in parentheses are standard error values, except for the process variance estimates which are 95% confidence intervals.

Demographic parameter	Tennessee	Ontario
Number of nests	102	86
Number of exposure days	1613	1234
Mean clutch size	4.30 (0.09)	4.95 (0.10)
Mean nest initiation date	May 13	May 23
Mean young fledged per successful nest	4.06 (0.13)	4.84 (0.15)
Daily nest survival rate (DSR)[a]	0.9717 (0.011)	0.9564 (0.019)
Nest success (DSR^{25}*100)	48.8%	32.8%
Fecundity[b]	1.50	1.33
Adult male survival (Φ)[a]	0.616 (0.111)	0.618 (0.084)
Male recapture/re-sighting rate (p)[a]	0.846 (0.096)	0.750 (0.085)
Adult female survival (Φ)[a]	0.427 (0.122)	0.477 (0.144)
Female recapture/re-sighting rate (p)[a]	0.623 (0.283)	0.664 (0.164)
Process variance (temporal) – Φ[a]	0.0261 (−0.0019–1.612)	0.0160 (0.0034–0.0897)
Lambda (λ)[c]	0.7468	0.7935

[a] Model averaged parameters estimates from Program MARK
[b] Mean number of young fledged × sex ratio × ($2p - p^2$) where $p = DSR^{25}$ and $2p - p^2$ accounts for one re-nesting attempt after a failed clutch (Giocomo 2005)
[c] Parameter estimated using PopTools in Microsoft Excel (Hood 2010)

breeding seasons for a total of 1,234 exposure days across a 50-day nesting season. No evidence of double-brooding was observed in either population. Mean clutch size for the Ontario population (4.95, range = 2–6 eggs, $n = 84$) was larger than the Tennessee population (4.30, range = 1–6 eggs, $n = 100$) ($t = 4.57$, $P < 0.001$). Likewise, the mean number of young fledged per successful nest in Ontario (4.84, $n = 47$) was larger than in Tennessee (4.06, $n = 60$) ($t = 3.87$, $P < 0.001$) (Table 1). In Tennessee, we color-marked between 21–35 males per year between 2003–2005, and 23 and 27 females per year in 2004–2005, respectively. In Ontario, we color-marked between 22–45 males per year and 15–33 females per year from 2001–2005.

Nest Survival

When we combined the nest survival data for both populations, the linear time trend model was most supported (Table 2, AIC_c weight = 0.55). The second most supported model was an additive model with linear time trend and region effect (AIC_c weight = 0.34, $\Delta AIC_c = 0.94$). The evidence that nest survival of Golden-winged Warblers varies between these two populations is limited; specifically, Ontario daily nest survival rates decrease throughout the nesting season at a slightly faster rate than Tennessee daily nest survival rates, but the confidence intervals for the DSR overlap considerably. All other models had ΔAIC_c values >4 indicating that they had little support, given the data and the model suite

TABLE 2. Summary of model selection results for Golden-winged Warbler (*Vermivora chrysoptera*) daily nest survival analyzed for Tennessee and Ontario data combined to assess regional effects. Columns provide model notation, the number of estimable parameters (K), second order Akaike Information Criterion (AIC_c), AIC_c differences (ΔAIC_c), and the relative likelihood of each model (AIC_c model weights; w_i).

Model	K	AIC_c	ΔAIC_c	w_i
Linear time	2	596.15	0.00	0.5491
Linear time + region	3	597.09	0.94	0.3429
Linear time + year	5	600.56	4.41	0.0605
Linear time + region + year	6	601.87	5.72	0.0315
Null (intercept only)	1	604.07	7.92	0.0105
Region	2	605.80	9.65	0.0044
Year	4	609.11	12.96	0.0008
Region + year	5	610.99	14.84	0.0003

TABLE 3. Summary of model selection results for Golden-winged Warbler (*Vermivora chrysoptera*) daily nest survival analyzed separately for the Cumberland Mountains of Tennessee (2004–2006) and the Canadian Shield in Ontario (2003–2006). Columns provide model notation, the number of estimable parameters (K), second order Akaike Information Criterion (AIC_c), AIC_c differences (ΔAIC_c), and the relative likelihood of each model (AIC_c model weights; w_i).

	Model	K	AIC_c	ΔAIC_c	w_i
Tennessee	Null (intercept only)	1	318.35	0.00	0.2095
	Minimum daily temperature	2	318.43	0.09	0.2007
	Linear time	2	318.99	0.65	0.1516
	Quadratic time	3	319.52	1.17	0.1168
	Year	3	320.08	1.73	0.0883
	Daily precipitation.	2	320.10	1.76	0.0870
	Nest age (linear)	2	320.35	2.01	0.0769
	Nest age (quadratic)	3	321.93	3.59	0.0349
	Nest stage	3	321.99	3.65	0.0338
	Global	8	330.22	11.87	0.0006
Ontario	Linear time	2	277.03	0.00	0.6427
	Quadratic time	3	279.04	2.01	0.2354
	Global	8	282.32	5.29	0.0457
	Year	3	283.24	6.20	0.0289
	Nest age (quadratic)	3	284.27	7.24	0.0172
	Daily precipitation	2	284.70	7.67	0.0139
	Nest age (linear)	2	286.59	9.56	0.0054
	Nest stage	3	286.72	9.69	0.0050
	Null (intercept only)	1	287.40	10.37	0.0036
	Minimum daily temperature	2	288.40	11.37	0.0022

considered (Table 2). In both populations, the majority of nest failures were attributed to predation (>95%) as opposed to other factors (e.g., weather or trampling by ungulates).

For the Tennessee population analyzed separately, the constant survival model was the most supported (AIC_c weight = 0.21), indicating that daily nest survival of Golden-winged Warblers may not vary significantly as a function of the modeled parameters. However, several other models (minimum temperature, year, daily precipitation, and linear and quadratic time) had ΔAIC_c values <2, providing some evidence for nest survival variation with these parameters (Table 3). While these relationships may exist, the 95% CI for the parameter estimates for all covariates included zero and the constant survival model performed best. The model-averaged estimate for daily nest survival rate of Golden-winged Warblers in Tennessee was 0.9717 (SE = 0.011) and the overall nest success ($DSR^{25} * 100$, where 25 = the number of days in the nesting cycle) was 48.8% (Table 1).

For the Ontario population analyzed separately, the linear time model had the most support given the data (AIC_c weight = 0.64), with daily nest survival decreasing over time. The parameter estimate from the linear time model was ß = −0.056 (95% CL = −0.086 to −0.025). The quadratic time model also had some support (AIC_c weight = 0.24, ΔAIC_c = 2.01), but all remaining models had ΔAIC_c values >5 (Table 3), indicating little support given the data (Burnham and Anderson 2002). The model-averaged estimate for daily nest survival rate of Golden-winged Warblers in Ontario was 0.9564 (SE = 0.019), and the overall nest success ($DSR^{25} * 100$) was 32.8% (Table 1).

Adult Survival

When we combined the adult survival data for both populations, the most supported models suggested that year and sex affect adult survival and re-sighting rate; no models with a region effect were supported (Table 4). The most supported model indicated a sex by year interaction effect on adult survival and a year effect on re-sighting rate (AIC_c weight = 0.48) and the second most supported model suggested a year effect on survival and a sex by time interaction on re-sighting rate (AIC_c weight = 0.21). Because we found no regional effect on adult survival and

TABLE 4. Summary of model selection results for Golden-winged Warbler (*Vermivora chrysoptera*) annual adult survival (Φ) and re-sighting probability (p) using data from Tennessee and Ontario combined to assess regional effects. Columns provide model notation, the number of estimable parameters (K), second order Aikaike Information Criterion (AIC_c), AIC_c differences (ΔAIC_c), and the relative likelihood of each model (AIC_c model weights; w_i).

Model	K	AIC_c	ΔAIC_c	w_i
$\Phi_{sex*year}\ p_{year}$	14	1040.35	0.00	0.4759
$\Phi_{year}\ p_{sex*year}$	14	1042.03	1.68	0.2058
$\Phi_{sex*year}\ p_{sex}$	12	1042.38	2.03	0.1728
$\Phi_{sex*year}\ p_{sex*year}$	18	1042.78	2.43	0.1415
$\Phi_{sex}\ p_{sex}$	4	1051.99	11.63	0.0014
$\Phi_{sex}\ p$	3	1052.96	12.61	0.0009
$\Phi_{region*sex*year}\ p_{region*sex*year}$	28	1053.02	12.67	0.0008
$\Phi_{region*sex}\ p_{sex}$	6	1054.37	14.01	0.0004
$\Phi_{region*sex}\ p$	5	1054.78	14.43	0.0004
$\Phi_{region*sex}\ p_{region*sex}$	8	1057.13	16.78	0.0001
$\Phi_{year}\ p_{year}$	9	1059.59	19.24	0.0000
$\Phi\ p$	2	1076.42	36.07	0.0000
$\Phi_{region}\ p$	3	1077.09	36.74	0.0000

re-sighting probability, the results from the survival analysis for each region run separately did not provide any additional information and so the AIC model results are not shown. We did use the region specific models to calculate model-averaged estimates of survival and re-sighting probabilities as well as estimates of temporal process variance for each region (Table 1).

Lambda Estimation

We estimated lambda for the Tennessee population as 0.7468 and for the Ontario population as 0.7935, suggesting that both populations were declining unless mortality and dispersal were being offset by immigration. For both the Tennessee and Ontario populations, after-second-year (ASY) survival (birds not in their first year of life) had greater elasticity values, however all four matrix elements had relatively similar values (Table 5).

DISCUSSION

Our demographic comparison of two populations of Golden-winged Warblers separated by ~1,000 km shows that despite larger clutch sizes and number of young fledged per nest in the northern population, nest survival and the resulting fecundity estimates were greater in the southern population. We also found that annual adult survival and population growth rate (λ) were similar between populations. Our predictions regarding demographic differences between Ontario and Tennessee Golden-winged Warbler populations were not fully supported; we expected birds in Ontario to have higher fecundity. Our fecundity prediction was partially based on an expectation of lower nest predation rates at higher latitudes (Ricklefs 1969, Kulesza 1990, Martin 1995), but we did not find this to be the case (Table 1). One explanation for this might be that the Ontario study area had a higher degree of agriculture in the surrounding landscape where nest predation rates may be higher (Rodewald 2002; but see Cottam et al. 2009, Riddle and Moorman 2010).

TABLE 5. Parameter values for the two-stage Leslie matrices for populations of Golden-winged Warblers (*Vermivora chrysoptera*) in Tennessee and Ontario, and the associated elasticity values for each matrix element. Annual After Second-Year (ASY) survival estimates (Φ) are for adult females estimated using Program MARK (see Table 1) and SY (Second Year) annual survival (during first year of life) is assumed to be half of ASY survival. Fecundity estimates are listed in Table 1 multiplied by the annual survival for SY and ASY birds.

	Parameter	Estimate	Elasticity
Tennessee	ASY Φ	0.427	0.327
	SY Φ	0.214	0.245
	ASY fecundity	0.640	0.245
	SY fecundity	0.320	0.183
Ontario	ASY Φ	0.477	0.361
	SY Φ	0.239	0.240
	ASY fecundity	0.633	0.240
	SY fecundity	0.317	0.159

Nest Survival

Our model results suggest that daily nest survival rates of Golden-winged Warblers in Tennessee may be negatively related to daily minimum temperature and time throughout the nesting season, but the null model was most supported. Ontario nest survival also decreased throughout the nesting season, but not as a function of temperature. Small mammals (Söderström et al. 1998) and snakes (Thompson and Burhans 2003, Weatherhead and Blouin-Demers 2004) make up the dominant nest predator community for ground-nesting birds such as Golden-winged Warblers. These predators are common on our study sites because of the dense cover of herbaceous vegetation, and snakes do not typically become active until later in the season (Stake et al. 2005, LB and RV, pers. obs.), when temperatures are greater and more food is available. Our data suggest that daily nest survival may decrease over time (and with increasing temperature in Tennessee); temporal variation in predation pressure may be a mechanism that drives this relationship (Sperry et al. 2008).

Adult Survival

Our prediction that the Tennessee population would have greater adult survival was not supported; Tennessee and Ontario male and female adult survival rates did not greatly differ (Table 1). Perhaps adult survival is not as influenced by latitude or alternatively, the significant variation in survival rates among individuals makes us less able to detect patterns as readily as with clutch size.

Accurate estimates of apparent survival are important for understanding population dynamics and choosing the best strategy for maintaining populations of conservation concern (Knutson et al. 2006). However, robust survival estimates are uncommon as they require relatively long term studies which involve intensive and time consuming recapture/resighting of individuals. Furthermore, several confounding factors must be considered that may bias our survival estimates low, including permanent emigration and lack of site fidelity (Marshall et al. 2004) seen more often in females and young birds. For example, a study of Yellow Warblers (*Setophaga petechia*) along a river corridor in Montana demonstrated that adult survival probabilities increased 6–22% when emigration was considered and these dispersers typically moved less than 300 m from their original location (Cilimburg et al. 2002). Because our study sites were discrete patches and not a continuous river corridor, dispersal distances and frequencies were likely greater for Golden-winged Warblers. We surveyed an additional 40 sites within 20 km of the focal sites with potentially suitable habitat during 2005 and 2006 in Tennessee and recorded the location of all banded and unbanded golden-winged males. During these surveys, we documented few dispersal events (n = 2 in 2005, n = 5 in 2006), and all were juveniles. A small number of adult dispersers were also recorded between core study sites (n = 1–3 individuals per year), but overall site fidelity was very high. Similar results were found in the population in Ontario where systematic (albeit road-based) surveys were conducted in the area surrounding the study sites from 2002–2004. While numerous Golden-winged Warblers were sighted, none of these surveys yielded birds already banded. Separating dispersal from mortality is difficult, especially when permanent emigration is known to occur, such that apparent survival rates underestimate true survival (Marshall et al. 2004, Anders and Marshall 2005). This is especially true for females and returning juveniles, because their site fidelity and detection is lower (Greenwood and Harvey 1982, Drilling and Thompson 1988, Clarke et al. 1997, Hansson et al. 2002, Sillett and Holmes 2002); however, research has also demonstrated that these individuals may have higher annual mortality (Liker and Székely 2005), specifically during migration (Woodrey and Moore 1997, Woodrey 2000) and on the non-breeding grounds (Marra and Holmes 2001, Latta and Faaborg 2002).

Apparent annual survival estimates for migratory songbirds encompass survival not only on the breeding grounds but also during migration and on the non-breeding grounds where they spend >50% of their annual cycle. Indeed, mortality events during the long migrations between breeding and non-breeding grounds likely account for >85% of adult annual mortality in Neotropical migratory songbirds (Sillett and Holmes 2002, Jones et al. 2004). The winter distribution of Golden-winged Warblers is from northern Columbia to Guatemala (Confer et al. 2011) where they occupy mid- to high- elevation woodlands and a variety of early successional habitats (Stiles and Skutch 1989). Beyond this, knowledge about their non-breeding ecology is

limited (but see Chandler and King 2011). Studies that assess overwinter survival and whether non-breeding habitat use differs by age class or sex (Marra 2000, Marra and Holmes 2001) would be useful in this species and would help to determine if availability of high-quality habitat is limiting populations and directly affecting annual adult survival. Further, knowledge of the level of migratory connectedness and the degree of habitat destruction throughout the non-breeding range will lead to a better understanding of how winter habitat availability may limit populations of Golden-winged Warblers.

Lambda Estimation

Our estimates of lambda for both Ontario and Tennessee Golden-winged Warblers suggested that these populations are declining rapidly at a rate of 20% and 24% per year, respectively. Breeding Bird Survey (BBS) data indicate these populations are indeed declining, but to a lesser degree (Sauer et al. 2011). From 2000–2005, there were too few BBS routes with occurrences of Golden-winged Warblers in Tennessee to get a trend estimate, but their populations have declined 7.86% per year ($P = 0.01$, $n = 4$ routes) from 1990–2006 (Sauer et al. 2008) in the southeastern region of the United States. Likewise, from 1990–2006, Ontario golden-winged populations have declined 8.01% per year ($P = 0.04$, $n = 28$ routes; Sauer et al. 2008). The number of breeding pairs remained relatively stable over the study periods in both study areas in Ontario and Tennessee, which does not corroborate a 24% annual decline. Our study sites represent high-quality habitat that likely receive immigrants on a regular basis, and therefore regional declines may not be detectable in the habitats where we conducted this research. In fact, un-banded individuals arrived on our sites each breeding season. We are unsure where these immigrants are dispersing from, but they may be juvenile dispersers hatched in the same region or individuals from nearby populations.

In addition to focusing on habitats with significant levels of immigration, the inconsistency between our lambda estimates and BBS trend estimates may be because our adult survival estimates were underestimated as a result of low female site fidelity. Permanent emigration is occurring, yet it appears to be at low levels. Tennessee adult female survival would need to be 0.565 (which is closer to our estimates for male adult survival), with known fecundity, to achieve a stable population ($\lambda = 1$). This is a difference of 0.143 or a 33.5% underestimate. Likewise, survival of adult females in Ontario would need to be 0.599, a difference of 0.122 or a 25.6% underestimate. Although such differences seem large, Marshall et al. (2004) demonstrated true survival for Prothonotary Warblers (*Protonotaria citrea*) was underestimated by 0.17 for males and 0.19 for females when dispersal events were not considered. The probability of dispersal and dispersal distance, therefore, are important demographic parameters that must be estimated explicitly for these populations to obtain unbiased estimates of survival. While we did not estimate the probability of dispersal explicitly, as mentioned earlier, we did search potentially suitable habitat within a very large area (~5% of an 800 mile^2 area) and found little evidence of dispersal in either population.

Conclusion

The lack of significant differences in demographic rates in Golden-winged Warblers in the northern and southern extremes of its breeding range (outside of expected differences in clutch size) has ecological and conservation implications. To our knowledge, only one other published study (Mattsson et al. 2011) has assessed latitudinal differences in intra-specific demography for a Neotropical migratory songbird. In this study, they assessed reproductive parameters (not adult survival) and found Louisiana Waterthrushes (*Parkesia motacilla*) were more likely to double brood and lay larger clutches in replacement nests in Pennsylvania compared with Georgia, but found no differences in clutch size or nest survival rates (Mattsson et al. 2011). Our results suggest that differences may not exist (or may not be detectable) for these birds when studied only on the breeding grounds, especially with regard to annual adult survival rates. Factors throughout the entire annual life cycle affect these species demographically. Our results suggest that limiting factors on the non-breeding grounds are similar for Golden-winged Warblers breeding in Tennessee and Ontario; future studies of migratory connectivity and non-breeding season habitat use are essential if we are to understand the demographic consequences of habitat loss on the non-breeding grounds (Rubenstein et al. 2002, Norris et al. 2006).

Both the populations in Ontario and Tennessee appear to be declining (based on our lambda

estimates as well as long term BBS data; Sauer et al. 2011), and conservation strategies may need to be tailored for each region specifically. However, we found few major differences among the populations suggesting that similar strategies in these two regions may be sufficient, at least until we find differences in the nest predator community or the degree of migratory connectedness. Our ability to influence daily nest survival rates may be currently limited by our knowledge of the predator communities, and because predation is a complex and dynamic process. Elasticity values for both populations were highest for adult survival, suggesting that this may be where we should focus our conservation efforts. However, annual adult survival is not typically affected by factors on the breeding grounds where monthly survival rates are high (Sillett and Holmes 2002, Jones et al. 2004). As a result, our best option for conservation of Golden-winged Warblers on the breeding grounds, considering the ephemeral nature of early successional shrublands, is the creation and maintenance of high-quality breeding habitat.

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HOME RANGE EXTENSION AND OVERLAP OF THE ORNATE TINAMOU (*NOTHOPROCTA ORNATA*) IN AN ANDEAN AGRO-ECOSYSTEM

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ABSTRACT.—Very little is known about the home range and movement patterns of tinamous. The Ornate Tinamou (*Nothoprocta ornata*), a species of the central Andes that is important for cynegetic and biomonitoring purposes, was previously reported to have a very small territory (2.43 ha). This was based solely on field observations. In order to gain a better understanding of the movement patterns, home range size, and home range overlap of this species, we radio tracked 12 adult individuals in an Andean agro-ecosystem for a full year. The birds remained within their home ranges all year; 100% MCP (minimum convex polygon) home ranges were 43.8 ± 21.6 ha (22–85 ha), 95% kernel home ranges were 58.8 ± 31.9 ha (25–118 ha) and 50% kernel core areas were 15.3 ± 8.9 ha (6–33 ha). Only two birds, probably sub-adults, showed extensive movement patterns before their death. Individuals overlapped their home ranges extensively (from 30–98% with 2–3 tagged individuals), but these values were probably higher because a small proportion of the population was tagged. No sexual differences were detected in home range size or overlap. Our results support the usefulness of Ornate Tinamou as a sentinel species in biomonitoring studies and highlight the need for further research into the philopatric and dispersion behavior of juveniles before planning cynegetic strategies. *Received 21 September 2012. Accepted 20 March 2013.*

Key words: cynegetic use, Neotropical region, radio tracking, sentinel species, Tinamidae, triangulation.

Tinamous are among the least studied bird species, despite their evolutionary, ecological, and cynegetic importance in Latin American countries. Basic ecological knowledge about their population density, abundance, home range size, movements, and dispersion patterns are important in order to develop management strategies.

Early studies on tinamous that focused on their movements, home range sizes, and home range overlap were based on field observations of few individuals (Schäfer 1954; Pearson and Pearson 1955; Lancaster 1964a, b). The home ranges reported varied from 0.1 ha in the Highland Tinamou (*Nothocercus bonapartei*) (Schäfer 1954) to 24 ha in the Brushland Tinamou (*Nothoprocta cinerascens*; Lancaster 1964a). To date, only one study on home range has used the radio-tracking technique and reported mean home range sizes of 16 and 19 ha for the Spotted Nothura (*Nothura maculosa*; Thompson and Carroll 2009). In general, tinamous are considered resident, non-migratory species, with the probable exception of the genus *Tinamotis* (Cabot 1992, Davies 2002).

Using existing knowledge about the general residence parameters and the relatively small home range sizes of tinamous as a starting point, Garitano-Zavala et al. (2010) proposed two tinamou species as potential sentinel species of chemical hazards produced by mining activities in the Andean region. The tissue concentrations of trace metals in the birds captured in polluted mining areas were significantly higher than those captured in control areas (Garitano-Zavala et al. 2010). In order to gain a better understanding of the relationship between the trace metal tissue concentrations and the pollutant dynamics in the environment in which they live, it is essential to find out about the movements, home range sizes, and home range overlap of these tinamou species. If several individuals are resident in relatively small and overlapping home ranges, the trace metal concentrations in the tissues of the birds will reflect exposure to soil, water, or food pollution on a local level.

One of these two species is the Ornate Tinamou (*Nothoprocta ornata*), which inhabits the South American Andes from southern Peru to northern Chile and Argentina at altitudes that range from 2,500–4,800 m (Cabot 1992, Davies 2002). The only previous studies on home range size and movements for this species were based on field

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observations by Pearson and Pearson (1955), who reported a nesting and feeding territory of 2.43 ha (6 acres) for a nesting pair, which would also suggest that this species is territorial and resident.

The highly variable reports concerning the home ranges of tinamou species, especially the small area previously reported for the Ornate Tinamou, require new studies in order to obtain more reliable measurements of home range and residence parameters.

Although it has been postulated that radio transmitters could negatively affect birds and may result in biased data (Barron et al. 2010), studies with ecologically similar bird species have demonstrated no negative effects (Hernández et al. 2004, Palmer and Wellendorf 2007, Terhune et al. 2007). We consider that radio tracking is not only adequate, but may be the only way to study tinamous in the field, given their reserved behavior (Cabot 1992, Davies 2002, Brennan 2004). The aim of the present study was to gain an insight into the movements, home range size, and home range overlap of the Ornate Tinamou by means of year-round monitoring of several radio-tagged sympatric males and females in a typical Andean agro-ecosystem on the Bolivian high plateau.

METHODS

Study Area.—We captured and studied wild Ornate Tinamou individuals in Qurpa (16° 40′ S, 68° 51′ W; 3,850 to 4,100 m asl), a rural locality on the Bolivian high plateau east of the Desaguadero River and south of Lake Titicaca. The total surface area used for radio tracking was approximately 820 ha. The climate is cold all year round, with greater daily than seasonal temperature fluctuations (minimum average monthly temperature 5.7 °C; maximum average monthly temperature 9.9 °C), dry in winter (minimum average monthly precipitation 5.1 mm) and rainy in summer (maximum average monthly precipitation 133.7 mm; SENAMHI 2012).

The mountainous landscape is a heterogeneous mixture of Andean crops (barley, bean, alfalfa, potatoes, oca, onion and quinoa, with no fields larger than a quarter of a hectare), interspersed with recently harvested and fallow fields and non-agricultural lands. The non-agricultural areas have bunch grasses, including *Stipa ichu* and *Festuca* spp., with a mixture of spiny and resinous shrub vegetation (e.g., *Baccharis incarum*, *Adesmia miraflorensis*, *Tetraglochin cristatum* and *Satureja boliviana*) and scattered rocky patches. These non-agricultural areas are used for grazing sheep, llamas and cattle. Several weed species grow in both the active and inactive agricultural areas. Crops are grown on an annual basis: sowing takes place between September and January, followed by the crop harvest between May and July, and the fields are then left ploughed for the next sowing season.

Evaluation of Effects of Radio Tagging.—We selected 12 g necklace tags (R1–2D model, Holohil System, Carp, Ontario, Canada) with a 24-month lifespan that represent 2.7% of the minimum adult body weight reported for this species (Davies 2002). Necklaces are the most common tagging system used for game birds (e.g., Novoa et al. 2002, Oakley et al. 2002, Pérez et al. 2004, Watson et al. 2007) that have the same size and ground-dwelling habits as the Ornate Tinamou, and were used successfully with the Spotted Nothura in a study by Thompson and Carroll (2009). Necklaces are recommended for bird species that do not fly frequently (Marcström et al. 1989, Kenward 2001). Studies on the ecologically similar but smaller Northern Bobwhite (*Colinus virginianus*) demonstrated that these radio transmitters had no negative effects on energy level (Hernández et al. 2004) or survival (Palmer and Wellendorf 2007, Terhune et al. 2007).

To evaluate the effects of tagging on the Ornate Tinamou (Murray and Fuller 2000), we attached necklace tags to three adult individuals (two females and one male) that were born and bred in captivity in the city of La Paz (3,450 m asl). These birds were held with seven other individuals in an enclosure measuring 8 × 5 m. To imitate the natural conditions in the wild, the enclosure had resinous shrub and bunch grasses, and the birds were exposed to natural weather conditions and fed mainly barley grains and alfalfa leaves, the largest and most frequently consumed items among wild individuals (Garitano-Zavala et al. 2003).

The necklaces were firmly attached to prevent tag loss over the head, and a gap of 7 mm was left between the elastic lace and the neck to avoid blocking the esophagus. For 6 months we observed the birds' behavior. We looked for abnormal movements, food plugged in the esophagus, bills lodged in the lace (Sorenson 1989), antennae or tags becoming tangled in vegetation (Brennan 2004), and premature tag

TABLE 1. Individual code assigned to each radio-tagged Ornate Tinamou (a combination of the channel number and the sex, F: female or M: male), body mass, days tagged (days from the tag attachment until the end of the study, death, or signal loss), causes of individual signal loss (a: tag was found with signs of predation on the bird; b: tag was found with no signs of predation on the bird; c: tag was not found; NL: the tag was not lost until the end of the study), total days of radio tracking by triangulation (DRT-T) and total months of radio tracking by homing (MRT-H) and triangulation (MRT-T) are shown.

Individual code	Body mass	Days tagged	Causes of signal loss	DRT-T	MRT-H / MRT-T
05M	420	310	a	32	3 / 8
10M	510	308	NL	44	11 / 11
15M	505	32	a	4	0 / 1
20F	340	128	a	16	3 / 4
40F	530	374	NL	44	10 / 11
55F	650	270	b	36	8 / 8
60F	(*)	251	c	20	6 / 5
65F	740	308	NL	44	11 / 11
70F	595	309	NL	44	11 / 11
75M	330	23	a	8	1 / 1
90M	490	261	a	28	3 / 7
99M	570	309	NL	44	11 / 11

(*) Because of the stress suffered during capture, individual was released without being weighed.

loss. When we removed the tags, we examined the skin for wounds and lacerations. We weighed the three birds and three other untagged adult individuals (two females and one male) before and after the 6 experimental months to evaluate the tagging effect with repeated ANOVA measurements (Zar 2010). We did not consider sex, because the sample was small and little effect has generally been reported (Barron et al. 2010).

Radio Tracking.—We trapped 12 Ornate Tinamou individuals (six males and six females) between September 2006–March 2007 with a mobile trap technique that is used by local hunters in Qurpa. The technique involves two teams of three people; each team walks slowly and quietly through the hills, searching from high natural observatories for any movement that may reveal Ornate Tinamou individuals in the crops, bunch grasses, or shrubs. Once a bird is sighted, a member of the team runs close to the bird, causing it to hide and squat under grass or shrubs, but not to flush. Two other team members who know the exact position of the bird slowly walk up to it and gently place a cotton net attached to two 3-m poles over the vegetation under which the bird is hiding. Finally, the bird is incited to flush and becomes tangled in the net.

The equipment used for radio tracking comprised two sets of Telonics TR-4, Telonics "H" Adcock RA-2A antennae (Telonics Inc., Mesa, Arizona, USA), hand-held GPS units (Garmin eTrexVista, Garmin International Inc., Olathe, Kansas, USA) and compasses. For each trapped bird, we recorded the GPS position, date, time, body mass and sex (by cloacal examination). There is no reliable field method for accurately determining the bird's age. We attached necklace tags as we had for the captive birds and fitted a numbered metal ring on the left leg before releasing it at the same capture location. Handling took no longer than 10 mins. Tag VHF signals were within the range of 150–154 MHz. The code for each individual was the receiver's channel number plus sex (Table 1). Tag weight percentages ranged from 1.6–3.6%.

We radio tracked each bird using triangulation and homing. With three birds tagged between September and November 2006, we defined fixed triangulation points, taking into account accessibility and signal detection quality on two parallel routes. The first route (5.16 km) was at the road across the plain (approximately 3,860 m asl); the second route (4.02 km) was 2 km away on the mountain summits (between 4,070–4,270 m asl). On each route, we established seven fixed points. In order to obtain four consecutive bearings at each location as quickly as possible (Kenward 2001), we matched to each fixed point a neighboring point 50 m away, assuming that the movement of any bird in the time taken for the observer to move that distance was negligible.

The precision and accuracy of the telemetry system for triangulation were tested following the methods suggested by White and Garrot (1990)

and Withey et al. (2001). We attached three test transmitters to wooden posts at a height of 30 cm in the areas where Ornate Tinamou individuals were observed and/or captured. The mean distance between the test transmitters and fixed points was 1.69 ± 0.60 km. An observer who did not know the locations of the test transmitters obtained the bearings from all fixed points. We estimated the test transmitter positions using Location of a Signal Software 4.0 (LOAS 2009). To minimize the error of intersection of the triangulated bearing, we used only triangulations that showed an angle between the bird and the fixed points of between 60° and 120°.

The mean distance between the estimated locations and known test transmitter positions was 193.67 m (SD = 75.31), and the mean and standard deviation of bearing errors was −0.016° ± 12.21. Based on these results, we concluded that our triangulation system was not biased and was accurate enough to estimate home ranges and overlap, but not habitat or resource use, given the birds' highly heterogeneous mixture of small-surface habitats (Montgomery et al. 2011).

Twice a month, between December 2006 and October 2007, two observers (one per route) walked early in the morning in the same direction along the routes (NW to SE or SE to NW) and returned in the opposite direction in the afternoon. At each pair of opposite fixed points, the observers recorded bearings for each tagged bird. Bearings were taken simultaneously for each bird by means of walkie-talkies. The time taken to travel between each telemetry location was at least 20 mins, which was chosen to minimize dependency and to obtain an adequate sample size (White and Garrot 1990, Powell 2000). As fixed points were visited twice a day, it was possible to locate each bird 14 times per day and 28 times per month, but because of topography interference this maximum was reduced.

The homing technique (White and Garrot 1990) was carried out by one observer for a period of 14 months (Jan 2007 to Feb 2008), six times per month, each time for a different, randomly selected individual. Because of adverse weather conditions, fewer than six individuals were radio tracked during some months. Each individual was radio tracked every 2-3 months at the beginning of the study, but as the number of birds decreased because of predation or signal loss, this rate increased to almost one register per month for each individual. Table 1 shows the total number of homing months per bird. From sunrise to sunset, the selected bird was followed on foot by means of radio contact until visual contact using 10 × 25 binoculars was achieved. Every 10 mins, the observer obtained the GPS position, the bearing, and the exact distance (m) to the bird by using a Laser Rangefinder Bushnell Yardage Pro (Bushnell Performance Optics, Overland Park, Kansas, USA). The bird's position at each visual contact was determined with Location of a Signal Software 4.0 (LOAS 2009). As these sequential locations were not independent, we did not use them for home range estimation. We used the data to: 1) resight birds and evaluate the accuracy of the positions calculated using the triangulation method and construct a 100% MCP (Mohr 1947) with all homing locations using RANGES VII software (South et al. 2005); and 2) evaluate the eventual effect of time and season on the spatial distribution of the birds and graphically differentiate homing locations by month and time of day (morning was classed as 0700–1030, noon as 1130–1430 and afternoon as 1530–1830). Using this information, we defined the method of working with triangulation data for home range estimation.

Home Range Estimation.—We entered all bearings obtained for each bird by triangulation into the Location of a Signal Software 4.0 (LOAS 2009) to calculate the birds' locations. We excluded unacceptable locations and only accepted those that showed an angle between the bird and the fixed points from 60° to 120° and error ellipses ≤2 ha (although 80% of accepted locations had ≤1 ha error ellipses). To test the degree of spatiotemporal relatedness of the locations, we determined autocorrelation using Schoener's ratio t^2/r^2 (Schoener 1981), where t^2 is the mean squared distance between consecutive locations and r^2 is the mean squared distance from each location to the arithmetic mean coordinates of all locations, using RANGES VII software (South et al. 2005).

We calculated the home ranges with 100% MCP (Mohr 1947) and density contours of 95% using fixed-kernel estimator with *ad hoc* choice of *h* (Worton 1989), because both permit direct comparisons with other studies. We also estimated 50% kernel contours as core areas. Kernel estimators are sensitive to sample size, so we only calculated home ranges and core areas for birds with 40 or more locations, as recommended by Seaman et al. (1999). We obtained all home

range calculations using RANGES VII software (South et al. 2005) and assessed sex differences using the non-parametric Mann-Whitney *U*-test, considering differences significant when $P < 0.05$ (Zar 2010).

We evaluated the total overlapping areas of individual home ranges (100% MCP) and core areas (50% kernel) using a Geographical Information System, ARCVIEW 3.2a (ESRI 1999), with which we obtained both the total overlapped surface area with certain individuals and the total overlapped area with all individuals versus the total free area. We performed sex comparisons using the Mann-Whitney *U*-test, considering differences significant when $P < 0.05$ (Zar 2010). For all statistical tests, we used PASW Statistics 18 (PASW 2009).

RESULTS

Effect of Radio Tags on Captive Individuals.—We did not detect any major effects of the tags on the three captive birds. No tags or antennae became tangled in the vegetation, nor were they lost prematurely. However, we did notice that the necklaces deteriorated, so they may have broken and gone missing if they had been used for a longer period of time. After we removed the tags, no bruises or lacerations were found on the skin that had been in contact with the radio tag. No individual's weight was significantly different after the 6 experimental months, for tagged or untagged individuals (factor before and after tagging: $F_{1,4} = 1.46$; $P = 0.29$; factor tagged and untagged birds: $F_{1,4} = 3.97$; $P = 0.12$).

Wild Radio-Tagged Birds Lost During the Study.—Only five of the 12 tagged birds kept the radio tag until the end of the study. The tags of the other seven birds were found in the field or the signal was lost, which occurred between 23 days and 10 months (Table 1). Five of these seven birds were probably depredated (representing 42% of the total tagged birds), because the transmitter was still emitting when found and feathers were scattered nearby. In addition, tooth marks were found on several transmitters, which led us to believe that the Andean fox (*Pseudalopex culpaeus*) killed these birds, although other predators such as the Colocolo cat (*Leopardus colocolo*), or even raptors such as the Black-chested Buzzard-Eagle (*Geranoaetus melanoleucus*) or the Variable Hawk (*Geranoaetus polyosoma*) may have been responsible. Of the other two tags, one was found in the field with no predation signs and the signal of the other was lost and the tag never found (Table 1).

TABLE 2. Total valid locations obtained by homing radio tracking for each Ornate Tinamou (F: female or M: male), area size, and total linear distance between capture site (C) and site of tag loss (L). NC = Data not calculated.

Individual	Locations	MCP 100% (ha)	Distance C-L (m)
05M	208	3	317
10M	935	11	
15M	0	NC	384
20F	212	34	1,522
40F	836	8	
55F	775	12	205
60F	370	111	1,184
65F	1,053	13	
70F	776	9	
75M	62	0.08	133
90M	197	6	121
99M	886	13	

Bird Movements.—Two birds (15M and 75M) died before we could obtain more than one month of homing and/or triangulation data (Table 1), and therefore it was not possible to identify their movement patterns. For eight of the other 10 birds, we did not observe any significant movements and therefore concluded that they were residents of a particular area. Homing data showed that the monthly and daily positions were equally distributed within the polygon area without any pattern, which would indicate the absence of any monthly or daily effects on bird location, and for the birds whose signal was eventually lost, the linear distances between capture and signal loss sites were less than 500 m (Table 2).

Only two birds showed a non-resident pattern and showed the maximum distances between the capture site and the site of tag loss (Table 2). Bird 20F (whose body weight suggested it was probably a sub-adult) moved 1,522 m northwest from the capture point in March 2007 to the point of tag recovery in July 2007. The homing 100% MCP was expressed in two polygons and triangulation locations were between the points of capture and death, which would suggest gradual movement. Bird 60F showed a large MCP area and a long distance between capture and last signal reception (Table 2). Locations revealed a monthly pattern, suggesting that this was a non-resident bird moving across a wide area before the signal was finally lost.

TABLE 3. Total radio tracked days, valid locations, home range (100% MCP and 95% kernel) and core area (50% kernel) size for each Ornate Tinamou (F: female or M: male) obtained using the triangulation method. t^2/r^2 is Schoener's ratio. NC = Data not calculated.

Individual	Valid locs.	100% MCP (ha)	95% kernel (ha)	50% kernel (ha)	t^2/r^2
05M	178	30	37	10	1.81
10M	113	85	118	33	1.50
15M	31	NC			
20F	55	NC			
40F	192	37	45	11	1.64
55F	100	26	34	8	1.72
60F	33	NC			
65F	86	63	91	22	1.63
70F	124	53	69	18	1.69
75M	21	NC			
90M	163	22	25	6	1.76
99M	71	34	51	14	2.07
Mean ± SD		43.8 ± 21.6	58.8 ± 31.9	15.3 ± 8.9	

Home Range Size and Core Areas.—We recorded locations for homing and their 100% MCP areas (Table 2). We calculated the home range and core area from year-round triangulation locations only for the eight birds that were resident and had more than 40 valid locations (Table 3). The locations of five of the eight birds were observed over a period of 11 months, and the total number of radio-tracking days was 44 (Table 1). Homing 100% MCP polygons were fully or mostly included in the triangulation polygons of 100% MCP and 95% kernel, which confirm that the accuracy of the positions calculated by triangulation was sufficient (Fig. 1). In addition, the calculated areas included the capture-release and tag-recovery points, or at least the points nearest to those areas (Fig. 1). Since Schoener's radius values for seven birds were between one and two, and for one bird, the value was just over two (Table 3), we considered the home range and core area calculations to be reliable.

We calculated individual and mean home ranges by 100% MCP and 95% kernel together with the 50% kernel core area (Table 3). We recorded sex-differentiated means (Table 4). In all cases, home range areas were bigger when calculated using the kernel method. Home ranges calculated by 100% MCP never exceeded 1 km^2 and ranged from 22–85 ha. Core areas ranged from 6–33 ha. No significant sex differences were found in 100% MCP ($z = -0.58$; $P = 0.56$), 95% kernel ($z = -0.29$; $P = 0.77$) or core areas ($z = -0.29$; $P = 0.77$).

No positive correlation was found between the total number of locations and the home range size (100% MCP: $r_s = -0.21$; $P = 0.61$; 95% kernel: $r_s = -0.38$; $P = 0.35$) or core area ($r_s = -0.38$; $P = 0.35$). Therefore, we believe that the number of locations was sufficient to carry out the calculations.

The eight tagged birds formed two clusters in the study area, both consisting of four birds (two males and two females) separated in two parallel valleys (Fig. 2). The presence of the birds in these clusters does not necessarily mean that they were paired.

Home Range Overlap.—All the individuals, regardless of sex, overlapped their home range with two or three other tagged males or females (Table 5, Fig. 2). The mean proportion of the total area of home range overlap was greater than 50% (Table 5); most individuals overlapped their core area with the same individuals that overlapped their home ranges, but to a lesser degree. During the homing, we observed untagged birds feeding, walking, or flushing in the home ranges of tagged birds (up to nine individuals feeding together in the non-reproductive season), so the proportion of overlap was actually greater.

The maximum overlap values detected were between male 10 and female 70 (Table 5, Fig. 2), which were a pair, according to homing observations. No other pairs of radio-tagged males and females were observed.

There was a wide variation in the occurrence and proportion of the home range and core area overlap between birds, but the patterns were not determined by sex. There was no difference between the proportion in which the total

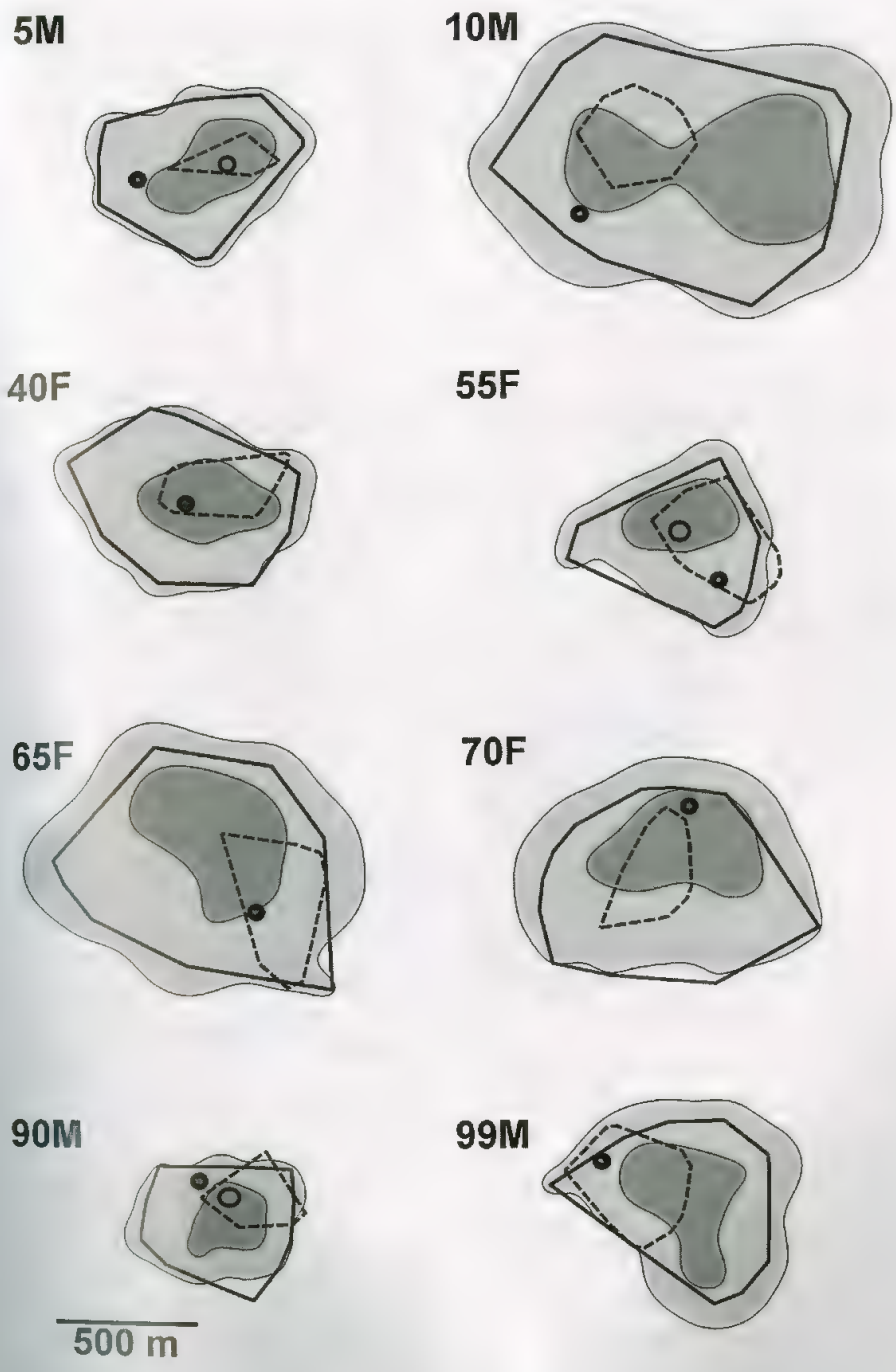

FIG. 1. Home range shapes of the eight birds for which home range calculation was possible. Continuous lines show 100% MCP using the triangulation method; dashed lines, the MCP obtained by homing locations; soft gray areas show kernel 95% home range; and dark gray areas, 50% kernel core areas. The closed circle shows capture point and the open circle shows tag recovery location.

TABLE 4. Year-round home range (100% MCP and 95% kernel) and core area (50% kernel) mean ± standard deviation for Ornate Tinamou males and females in the Bolivian Andes.

	100% MCP (ha)		95% kernel (ha)		50% kernel (ha)	
Group	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Male (n = 4)	43 ± 29	22–85	58 ± 42	25–118	16 ± 12	6–33
Female (n = 4)	45 ± 16	26–63	60 ± 25	34–91	15 ± 6	8–22

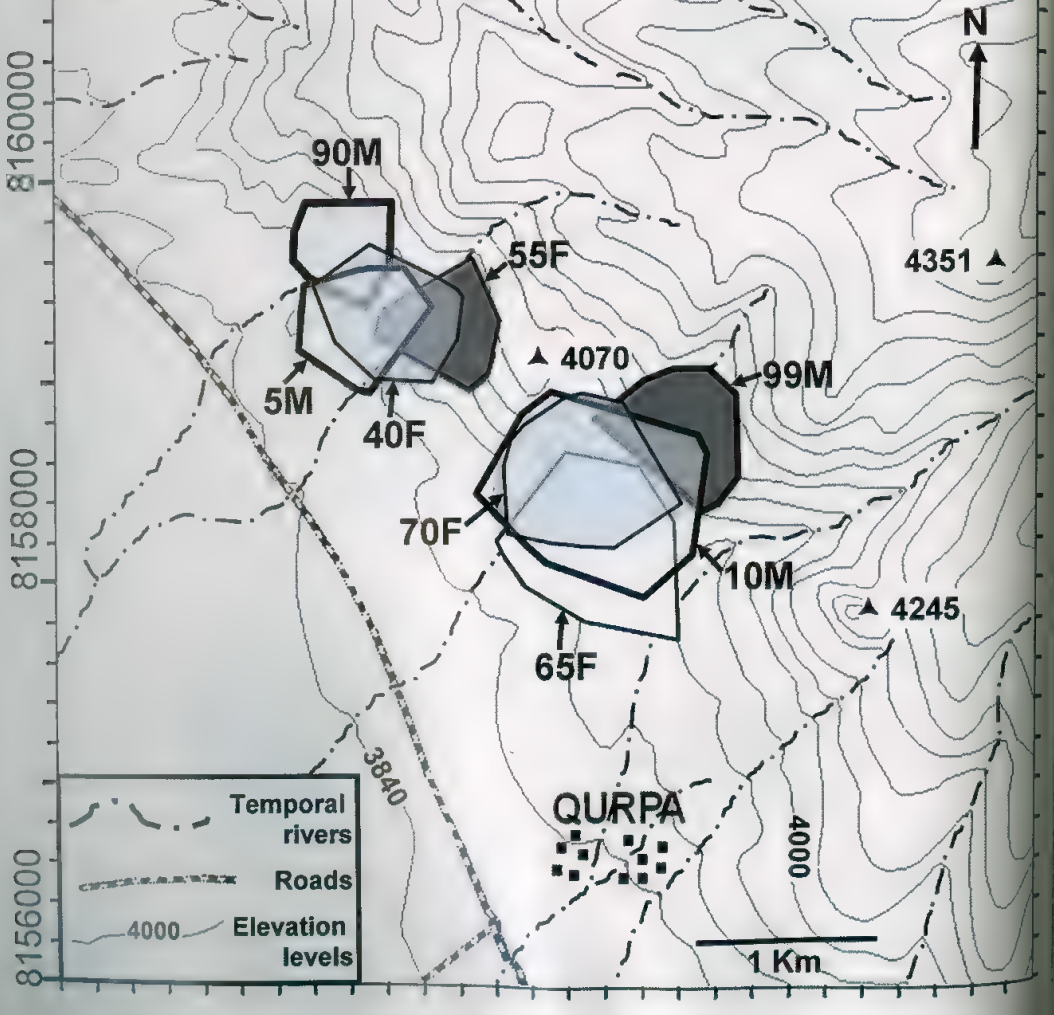

FIG. 2. Position in the study area and home range overlap (MCP 100%) of the eight birds for which home range calculation was possible (each polygon identified with the individual code). Bold-lined polygons are males; light-lined polygons are females.

TABLE 5. Total size, percentage of home range, and the number of other tagged individuals that overlap on the home range (100% MCP) and core area (50% kernel) of each individual Ornate Tinamou.

Individual	Total home range overlap 100% MCP			Total core area overlap 50% kernel		
	ha	%	Number of individuals	ha	%	Number of individuals
05M	21	71	3	6	57	2
10M	77	90	3	19	56	3
40F	33	88	3	8	77	2
55F	14	53	2	3	34	2
65F	43	69	2	13	59	2
70F	52	98	3	5	28	2
90M	6	30	2	0	0	0
99M	13	38	2	2	17	1
Mean ± SD	32 ± 24	67.1 ± 24.9		8 ± 6	41.0 ± 25.6	

individual home range size of males and females overlapped ($z = -0.87$; $P = 0.39$, for area and percentage) or that in which their core area overlapped ($z = -0.58$, $P = 0.56$ for area; $z = -1.16$, $P = 0.25$ for percentage). Moreover, males do not overlap differently with males or females ($z = -1.08$, $P = 0.28$ for home range area; $z = -1.07$, $P = 0.29$ for home range percentage, $z = -0.88$, $P = 0.38$ for core area; $z = -0.88$, $P = 0.38$ for core area percentage) nor do females overlap differently with males or females ($z = -0.43$, $P = 0.67$ for home range area; $z = 0.0$, $P = 1.0$ for home range percentage, $z = 0.0$, $P = 1.0$ for core area; $z = -0.21$, $P = 0.83$ for core area percentage).

DISCUSSION

The loss of 42% of the tagged birds (probably because of predation) is lower than other studies on ground-dwelling birds (which are common target species of several predators): 88% in adult-reintroduced Northern Bobwhites (*Colinus virginianus*; Oakley et al. 2002), 81% in Red-legged Partridge chicks (*Alectoris rufa*; Pérez et al. 2004) and 91% for the wild Spotted Nothura (Thompson and Carroll 2009).

The birds that died soon after being tagged had a lower body weight at the time of capture. Bird 75M did not live more than a month: it weighed 330 g and the tag represented 3.6% of its body mass at the time of capture (the highest percentage of all the tagged birds in this study). Bird 20F lived for 5 months and weighed 340 g (the tag represented 3.5% of its body mass). The weight of the birds that died later ranged from 420–505 g, unlike those that survived, whose body weight ranged from 510–740 g. Although some researchers failed to detect any effects caused by transmitters weighing less than 4% of body mass (Murray and Fuller 2000), and Barron et al. (2010) suggested little evidence of negative effects when tags exceeded 3%, it is important to consider a predation phenomenon linked to weakness or a lack of experience (if body mass is related to age).

The mean home range size (100% MCP) reported for the Ornate Tinamou in this study is approximately twice the highest home range values reported for other species in this family and approximately 20 times greater than the so-called 'nest and feeding territory' reported by Pearson and Pearson (1955) for the Ornate Tinamou. In another study that used radio-tracking technology for tinamous, Thompson and Carroll (2009) reported 100% MCP mean home range sizes from 16 ha (crop and grazing sites) to 19 ha (crop sites) for the Spotted Nothura. Although Thompson and Carroll (2009) did not report individual home ranges, they highlighted a great inter-individual variation, which is similar to our results for the Ornate Tinamou. Our minimum values of individual home range sizes of Ornate Tinamou correspond with those described for other tinamous in the literature.

However, the majority of the previous reports were conducted with direct or signal observations. For example, Schäfer (1954) used a hunting dog to assess home ranges and reported a very small territory of 0.1 ha for Highland Tinamou males and territories of 20 ha for the Gray Tinamou (*Tinamus tao*). Lancaster (1964a) reported home ranges between 17–24 ha for the Brushland Tinamou by detecting the individual songs of four males. The same author, using the same technique, reported home ranges between 11–19 ha for the

Red-legged Tinamou (*Crypturellus erythropus*; Lancaster 1964b).

We found a high percentage of overlap in home ranges and core areas; these values may be even higher, as only a small percentage of the population was tagged. A high proportion of overlap was reported for other tinamous. Lancaster (1964a) described an overlap in the home ranges of Brushland Tinamou males of approximately 75%, and similar findings for the Red-legged Tinamou (Lancaster 1964b).

The Ornate Tinamou adult individuals remained within their home ranges for a whole year, with no great movements. Therefore, individuals must be able to obtain resources within their home ranges, by taking advantage of both spatial (different habitat types on a small scale) and temporal (annual crop management) heterogeneity, which is closely associated with the generalist and opportunistic feeding behavior of this species (Garitano-Zavala et al. 2003).

Sentinel species provide useful data for understanding or predicting potential human health impacts from environmental contaminants (Stahl 1997). Wildlife species have a wide variation in distribution, and migratory, dietary and reproductive habits, which are fundamental factors when selecting a species as a sentinel organism (Fox 2001). The parameters related to home range size, residence overlap and dietary habits of the Ornate Tinamou show that individuals are at risk of coming into contact and ingesting the chemical hazards in polluted areas, and therefore it is possible to assume that the bio-accumulation patterns of chemical hazards are directly associated with the pollution characteristics of the area in which the individuals were captured. This highlights the usefulness of the Ornate Tinamou as a sentinel species for Andean mining activities, where pollutants such as trace metals can reach soils, and water from the tailing piles may contaminate the crops and water consumed by tinamous and humans (Garitano-Zavala et al. 2010).

From a cynegetic management point of view, our results suggest that adult individuals are sedentary. If residence in a particular area is maintained throughout all the bird's life, it is important to use caution when hunting activities are planned, because the recolonizing capacity of Ornate Tinamou adult individuals may be seriously limited. If this is the case, then local extinction would occur if hunting affected all of the individuals in an area. Moreover, the dynamics and dispersion capacity of juveniles need to be evaluated, because the great movements and premature deaths of some of the individuals we studied could be interpreted as sub-adult non-resident individuals not being established in a stable home range. Before planning sustainable cynegetic activities for this species, it is crucial to gain a better understanding of its recolonizing capacity from non-hunted areas.

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WINTER HABITAT ASSOCIATIONS OF FOUR GRASSLAND SPARROWS IN FLORIDA DRY PRAIRIE

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ABSTRACT.—North American grassland birds show long-term population declines that generally exceed the declines of other bird groups. Efforts to conserve grassland birds require knowledge of ecological and habitat requirements during both the breeding and nonbreeding periods of annual life cycles. Nonbreeding habitat associations may affect survival and the acquisition of resources needed for migration and breeding. We focused on the winter habitat associations of a suite of co-occurring grassland sparrows in the dry prairie of south-central Florida, an understudied region within the wintering range of Grasshopper Sparrows (*Ammodramus savannarum pratensis*) and Henslow's Sparrows (*A. henslowii*). During the nonbreeding winter months, these two migratory sparrows commingle with resident Bachman's Sparrows (*Peucaea aestivalis*) and federally endangered Florida Grasshopper Sparrows (*Ammodramus savannarum floridanus*). We investigated sparrow habitat associations within two defined plant communities of the dry prairie ecosystem, the dry-mesic and wet-mesic prairie, for four prescribed fire treatments over two consecutive winters. Grasshopper and Henslow's sparrows showed higher relative abundance in wet-mesic prairie and Bachman's Sparrows were more abundant in dry-mesic prairie across all fire treatments. Florida Grasshopper Sparrows were detected only in the first and second years post-burn; samples were too small to yield information on potential preferences between the two prairie communities evaluated. We used an information-theoretic approach to select models that best predicted abundances for each species (except Florida Grasshopper Sparrows) based on time since fire and plant community. Abundances of Grasshopper and Bachman's sparrows were best predicted by plant community association and secondly by time since fire; whereas for Henslow's Sparrows, habitat and time since fire were equally important. This is the first concurrent study of these four sparrow taxa in peninsular Florida and indicates that time since fire influences the habitat preferences exhibited by wintering sparrows, but that this role differs across co-occurring species and dry prairie plant communities. *Received 31 August 2012. Accepted 3 May 2013.*

Key words: Bachman's Sparrow, burn, fire, Florida Grasshopper Sparrow, Grasshopper Sparrow, Henslow's Sparrow, nonbreeding season.

Habitat loss and degradation are primary factors cited in the steady declines of grassland birds in North America, including Bachman's Sparrow (*Peucaea aestivalis*), Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*), the eastern North American subspecies of Grasshopper Sparrow (*A. s. pratensis*, hereafter, "Grasshopper Sparrow"), and Henslow's Sparrow (*A. henslowii*) (Delany et al. 1985, Sauer et al. 2011). Each of these sparrows is classified as a species of conservation concern in more than one North American region (USFWS 2008) and in several southeastern states that provide winter habitat for migratory Grasshopper and Henslow's sparrows (Sauer et al. 2011). Mitigating grassland bird declines requires better knowledge of their winter ecology, because winter habitat selection cues may differ from the cues used during the breeding season, and managing landscapes solely for favorable breeding habitat may ignore important wintering habitat needs (Vickery and Herkert 2001, Newton 2004, Macias-Duarte et al. 2009).

The dry prairie of south-central Florida is a predominantly mesic ecosystem that provides both breeding and nonbreeding habitat for grassland sparrows. The dry prairie is a treeless, pyrogenic mosaic of plant communities comprised of more than 20 plant species per square meter ($\bar{x}$ = 21.6 species/m^2; range 9 to 41 species/m^2) and up to 49 species per square meter in the wet calcareous community type, one of the highest plant species richness values globally at this spatial scale (Orzell and Bridges 2006a, b). Less than 10% remains of an estimated 5,000 km^2 of pre-settlement Florida dry prairie (Noss 2013).

Dry prairie is characterized by a predominance of saw palmetto (*Serenoa repens*), dwarf live oak (*Quercus minima*), and wiregrass (*Aristida stricta* var. *beyrichiana*). Relative abundance of these and other plants characteristic of dry prairie varies along a soil moisture gradient from graminoid-dominated wet-mesic and wet prairies to the more shrubby mesic, dry-mesic, and sub-xeric prairies. Plant communities within this heterogeneous

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mosaic can be distinguished by indicator species associated with segments of a wet to sub-xeric soil moisture gradient (Noss et al. 2008). Infrequent fire results in encroachment of woody shrubs and trees that shade out pyrogenic bunchgrasses, increased herbaceous density at ground level, and reduction or elimination of bare ground areas, which in turn impair movement, foraging efficiency, and predator detection by ground-dwelling sparrows (Vickery 1996, Bechtoldt and Stouffer 2005, Tucker et al. 2006, Cox and Jones 2009).

Lightning-ignited fires in Florida dry prairie occur approximately every two years, a rate among the highest in the world (reviewed in Noss 2013). Previous research on grassland sparrows emphasized relationships between sparrow abundance and the effects of fire frequency on vegetation structure and seed production. Fire frequency plays a key role in breeding habitat selection by Bachman's and Florida Grasshopper sparrows (Shriver et al. 1999; Shriver and Vickery 2001; Delany et al. 2002; Tucker et al. 2004, 2006), Henslow's Sparrows (Cully and Michaels 2000; Reinking et al. 2000; Powell 2006, 2008), and Grasshopper Sparrows (Powell 2006, 2008). Fire also plays an important role in wintering habitat selection for Henslow's Sparrows in Louisiana, Mississippi, Alabama, Georgia, and the western Florida panhandle (Tucker and Robinson 2003; Tucker et al. 2004, 2006; Bechtoldt and Stouffer 2005; Cox and Jones 2009; Palasz et al. 2010). Previous research suggested that winter survival of these grassland birds may be linked to fire frequency in overwintering habitat (Tucker and Robinson 2003, Thatcher et al. 2006), but other studies disputed this (Johnson et al. 2011). The effect of fire history on winter habitat selection of both the non-migratory Florida Grasshopper Sparrow (Dean 2001) and the migratory Grasshopper Sparrow (Butler et al. 2009) in Florida dry prairie has been studied, but no published information is available on winter habitat preferences of Henslow's or Bachman's sparrows in peninsular Florida. In fact, Christmas Bird Count records and published reports of Henslow's Sparrows in peninsular Florida are scarce (Robertson and Woolfenden 1992, Stevenson and Anderson 1994, Pranty and Scheuerell 1997).

We examined four co-occurring taxa of wintering grassland sparrows in Florida dry prairie over a two-year period. We hypothesized that the relative abundance of each sparrow taxon would relate to prairie plant community and to the number of growing seasons post-fire. Knowledge of relationships between winter habitat occupancy of co-occurring sparrows and plant communities in peninsular Florida will allow better predictions of sparrow occurrence and potential viability on a landscape scale and provide a basis for habitat restoration, species recovery, and land acquisition (Noss et al. 2008).

METHODS

Study Site.—We conducted our research at Kissimmee Prairie Preserve State Park, which encompasses approximately 10,200 ha of dry prairie within the 22,500 ha Preserve (USFWS 1999). During our 2006–2008 field research, the Preserve was believed to support one of the largest extant populations of endemic, non-migratory Florida Grasshopper Sparrows (Pranty and Tucker 2006), an abundant breeding population of Bachman's Sparrows, and several species of overwintering and migratory sparrows including Henslow's, Grasshopper, Savannah (*Passerculus sandwichensis*), Swamp (*Melospiza georgiana*), Chipping (*Spizella passerina*), and small numbers of Le Conte's (*Ammodramus leconteii*), Lincoln's (*Melospiza lincolnii*), and Vesper (*Pooecetes* gramineus) sparrows (P. Miller and MGK, unpubl. data).

Flush-Net Sampling.—We used flush-netting, an active sampling method in which birds are systematically driven toward a stationary line of mist nets for mark and recapture (Gordon 2000). Variations of the method involve systematic flushing of plots with individual birds flushed into a mobile mist net set up at the location of each flushed bird (Johnson et al. 2009, Palasz et al. 2010). We selected the flush-netting method to improve accuracy in identifying cryptic, closely related sparrows that might otherwise be misidentified in flight (Bechtoldt and Stouffer 2005). We assumed that all sparrows present were flushed at least once and counted or captured. We flushed sparrows using noisemakers (2 L plastic bottles containing pebbles) attached to a 30-m rope dragged over the vegetation by two observers toward a 120-m long mist net array centered within each established plot. A third observer walked behind the rope and marked sparrow flush locations with a numbered flag. The flag location was recorded with a hand-held Garmin Vista Cx GPS unit. The area sampled in each flushed plot was determined by recording WAAS-enabled GPS locations (<3 m error) at each end of the

TABLE 1. Sampling strategy for burn classes, each sampled in six plots of between 4–5 ha. Three of the six plots in each group covered predominantly wet-mesic prairie, and three plots covered predominantly dry-mesic prairie. An unscheduled burn of Five Mile Prairie occurred in the latter part of the first sampling year preventing resampling of those six plots. The total number of plots sampled (including replicate samples) in each year was 36.

	Sampling area	Burn class	# of plots	Times sampled	# of Plot samples
Year 1					
	Corridor Prairie	2	6	1	6
	Five Mile Prairie	2	6	1	6
	Audubon Prairie	2	6	2	12
	Duck Slough East Prairie	4	6	2	12
Year 2					
	5 Mile Prairie	1	6	3	18
	Audubon Prairie	3	6	3	18

mist net line and at one end of the 30-m rope at initiation of each flush transect. We calculated the relative abundance of each flushed sparrow species by burn class as the number of sparrows per 100 ha to adjust for variation in sample plot size. Although capturing flushed birds was not required for the research presented in this paper, we suggest that by doing so we were able to improve positive identification of other cryptic sparrows flushed but not captured.

Wet-Mesic Versus Dry-Mesic Prairie Habitat.—We adapted the dry prairie vegetation classification system developed by Noss et al. (2008) to two categories for this study. We defined dry-mesic prairie as populated predominantly by shrubs (e.g., *Serenoa repens*, *Quercus minima*, *Lyonia lucida*, *L. fruticosa*, *Hypericum reductum*, *Vaccinium myrsinites*, *Gaylussacia dumosa*, *Lechea torreyi*), with graminoids (e.g., *Sorghastrum secundum*, *Dichanthelium portoricense*, *Xyris caroliniana*) and non-woody forbs (e.g., *Carphephorus carnosus*, *Pityopsis graminifolia*, *Pterocaulon virgatum*). We defined wet-mesic prairie as populated predominantly by graminoids (e.g., *Ctenium aromaticum*, *Dichanthelium leucothrix*, *D. erectifolium*, *Xyris elliottii*, *X. ambigua*) and non-woody forbs (e.g., *Chaptalia tomentosa*, *Eriocaulon decangulare*, *Bigelowia nudata*, *Lachnocaulon anceps*). Wiregrass (*Aristida stricta* var. *beyrichiana*) is an abundant and characteristic grass across this habitat gradient (Orzell and Bridges 2006a, b). The same observer visually classified the vegetation within a 10-m diameter circle centered on each sparrow flush location (n = 239: 2006–2007; n = 316: 2007–2008) into one of the two habitat categories, either dry-mesic or wet-mesic, based on the presence of the selected plant indicator species (Noss et al. 2008).

Effects of Time Since Fire.—We defined burn class in this study as the number of growing seasons post-burn. Samples were taken from 27 October 2006 to 28 February 2007 (2006–2007 samples), and from 5 November 2007 to 11 March 2008 (2007–2008 samples). Migrants persisted at the study location into April or later, but flush-net sampling terminated in early March because of federal permit conditions prohibiting flush-netting in the breeding season of the endangered Florida Grasshopper Sparrow.

In the first year we sampled burn classes two and four, and in the second year burn classes one and three (Table 1); burn class sampling could not be replicated between years due to the biennial prescribed fire rotations implemented at the study site for recovery of the Florida Grasshopper Sparrow. Plots were established to ensure sampling of an approximately equal area of both dry-mesic and wet-mesic prairie within each burn class and were sized to permit systematic sampling of each plot in one work-day by a three-person field crew. Six plots, each approximately 4–5 ha, were selected in each burn class such that three plots in each group covered predominantly dry-mesic habitat and three plots covered predominantly wet-mesic habitat. Both habitat types were present to a varying extent in each plot because of the mosaic character of the dry prairie ecosystem. All plot groups were located in areas where Florida Grasshopper Sparrows were documented to be breeding in the season immediately before, after, or both before and after the winter sampling seasons.

In 2006–2007, three groups of six plots were established in burn class two prairies. One set of six plots was established in burn class four prairies. In 2007–2008, one set of six plots was

established in burn class one habitat, and one set of six plots was established in burn class three prairies. Due to biennial prescribed burn rotations in effect at the study site for the benefit of the Florida Grasshopper Sparrow, all samples from burn classes two and four were taken in 2006–2007, and burn classes one and three were sampled in 2007–2008 (Table 1).

A total of 36 plot samples were taken in each year, with 4–6 weeks between repeated samples of the same plot within a given year. Based on previous research (Carrie et al. 2002, Tucker and Robinson 2003, Butler et al. 2009, Johnson et al. 2009), we assumed that this time lapse was sufficient to consider sparrow locations in each plot as independent samples regardless of any within-season site fidelity by individual birds. Although research on wintering Henslow's Sparrows in longleaf pine habitat in southern Louisiana showed that radio-tagged birds remained within a 0.3 ha area for a period of up to three weeks (range 0.09–1.50 ha; $n = 16$ individuals using 11 locations per individual) (Bechtoldt and Stouffer 2005), we found no published literature suggesting that grassland sparrows that show fidelity to a winter home range were associated exclusively with a single plant community, so we assumed that sparrow flush locations indicated a preferred habitat association.

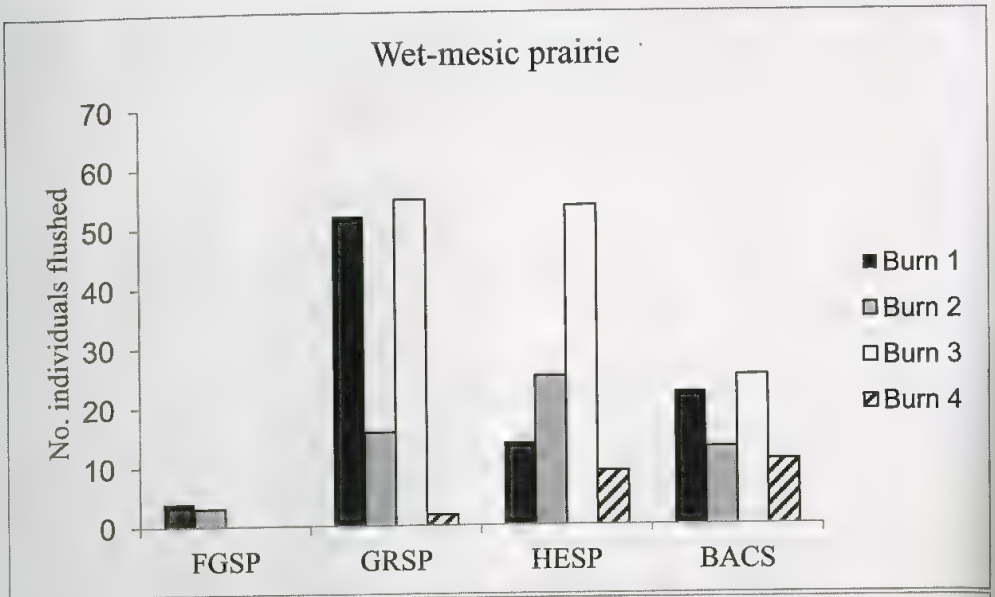
Statistical Analyses.—We used a 4 × 2 chi-square analysis to test for association between burn class and prairie habitat category (wet-mesic and dry-mesic) by species within each burn class. Florida Grasshopper Sparrows were excluded from the analyses for burn classes three and four, because the expected abundances were zero, a violation of the assumptions for chi-square tests. We used an information-theoretic approach (Burnham and Anderson 2002) to rank generalized linear models regressing predictor variables of burn class, habitat category, and interactions between these two variables against sparrow abundance by species. Because we could not replicate sampling of the same burn classes in both years, we simplified the analysis by calculating a combined relative abundance for each sparrow in each habitat category for burn classes one and two combined and for burn classes three and four combined. We obtained Akaike information criteria (AIC) scores for each candidate model using R statistical computing software (R Core Development Team 2012) and corrected these scores for small sample size (AIC_c). We calculated Akaike weights (w_i), relative likelihood (L_i), and number of model parameters (K) for each candidate model and ranked the model weights to select the models that best predicted abundance of each species.

RESULTS

Total area sampled in each burn class was 94.4 ± 1.9 (SD) ha for burn class one, 108.5 ± 1.3 (SD) ha for burn class two, 84.2 ± 1.9 (SD) ha for burn class three, and 55.6 ± 0.6 (SD) ha for burn class four. In 2006–2007 sampling, 134 sparrows were captured; an additional 105 sparrows were identified as one of the focal sparrow taxa when flushed but were not captured. In 2007–2008 sampling, 149 sparrows were captured; an additional 167 sparrows were identified as one of the focal taxa when flushed but were not captured. During the two winters of sampling, 130 Bachman's Sparrows were captured a total of 161 times, 10 Florida Grasshopper Sparrows were captured 13 times, 78 Grasshopper Sparrows were captured 90 times, and 74 Henslow's Sparrows were captured 86 times. Recaptured birds were caught only in the plots in which they were captured initially and not in any other sampled plot. The number of unidentified birds averaged one bird per 4.1 ha; flush-net plot size ($n = 36$) averaged 4.7 ± 0.52 (SD).

Florida Grasshopper Sparrows were captured only in one set of six plots in Five Mile Prairie in both years of this study (2006–2007, burn class two [$n = 5$]; 2007–2008, burn class one [$n = 8$]). None were detected in burn class three or four prairies. The set of plots in which Florida Grasshopper Sparrows were captured was within a core breeding area for the subspecies within Kissimmee Prairie Preserve. In 2006–2007, three individuals were flushed from wet-mesic prairie and two from dry-mesic prairie. In 2007–2008, four individuals were flushed from wet-mesic prairie and four from dry-mesic prairie (Fig. 1). Although sample sizes are prohibitively small for analyses, results suggest that Florida Grasshopper Sparrows have a wintering habitat preference for burn class one and two prairie over burn classes three and four. However, potential inferences regarding habitat preferences are limited, because birds were captured only in proximity to a core breeding area, whereas none were captured in other prairies where breeding also was documented during our research period.

Bachman's, Grasshopper (*A. s. pratensis*), and Henslow's Sparrows were flushed at all sites



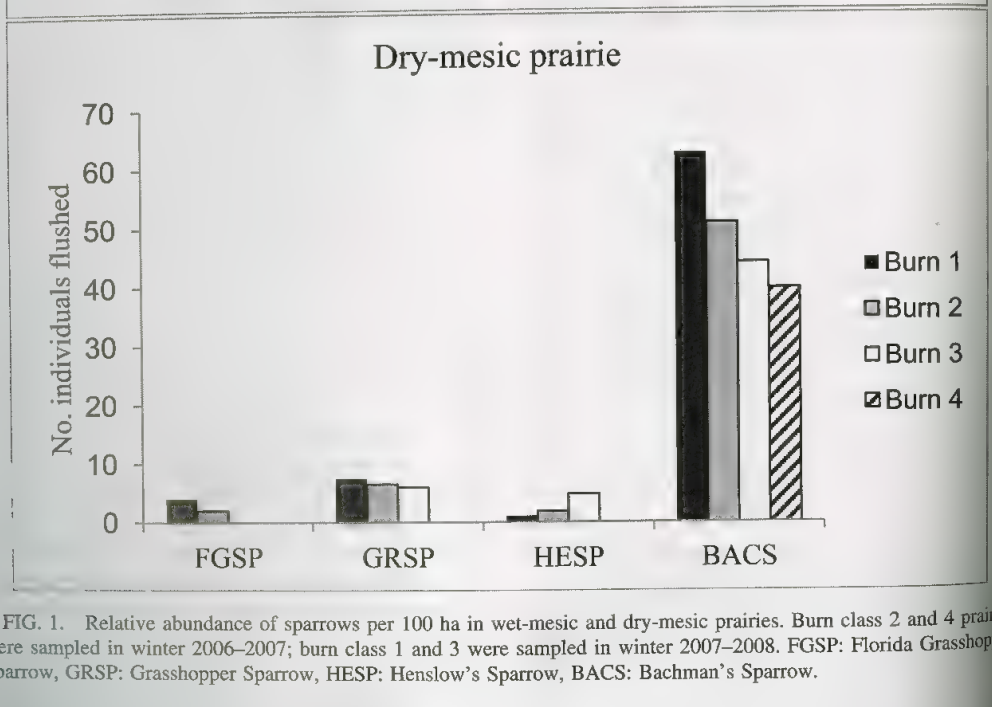


FIG. 1. Relative abundance of sparrows per 100 ha in wet-mesic and dry-mesic prairies. Burn class 2 and 4 prairies were sampled in winter 2006–2007; burn class 1 and 3 were sampled in winter 2007–2008. FGSP: Florida Grasshopper Sparrow, GRSP: Grasshopper Sparrow, HESP: Henslow's Sparrow, BACS: Bachman's Sparrow.

sampled in both winters; however, the latter two species were more abundant in wet-mesic prairie in burn classes one, two, and three than Bachman's Sparrows (Fig. 1). Bachman's Sparrows also favored burn class one and two patches, but were significantly more abundant in burn class four prairies than Grasshopper or Henslow's sparrows sampled in 2006–2007. Grasshopper and Henslow's sparrows were more abundant in wet-mesic than in dry-mesic patches in all burn classes sampled. In contrast, Bachman's Sparrows were more abundant in dry-mesic than in wet-mesic patches in all burn classes (Fig. 1). Overall each species showed a unique suite of responses to fire regimes that differed between wet and dry-mesic habitats.

TABLE 2. Results of 4 × 2 chi-square tests (all $P < 0.001$) demonstrate a lack of independence between sparrow abundance (birds/100 ha) and the two habitat categories within each burn class. FGSP: Florida Grasshopper Sparrow (*A. s. floridanus*), GRSP: Grasshopper Sparrow (*A. s. pratensis*), HESP: Henslow's Sparrow, BACS: Bachman's Sparrow.

Burn class	Sparrow	Wet mesic	Dry mesic	χ^2	df
1	FGSP	4	4	58.543	3
	GRSP	56	12		
	HESP	14	1		
	BACS	22	63		
2	FGSP	3	2	45.961	3
	GRSP	18	8		
	HESP	25	2		
	BACS	13	51		
3	FGSP	0	0	62.758	2
	GRSP	55	6		
	HESP	53	5		
	BACS	25	44		
4	FGSP	0	0	24.314	2
	GRSP	2	0		
	HESP	9	0		
	BACS	11	40		

Relative sparrow abundance was significantly associated with habitat category in all valid cases in which the expected abundance was not zero (all $P < 0.0001$; Table 2). This provides evidence that the four sparrow taxa sampled display different dry and wet-mesic habitat affinities that are also independent of burn class.

We used an information-theoretic approach to rank candidate models that predicted sparrow abundance as a function of burn class (burn classes one and two combined; burn classes three and four combined) and habitat category (dry-mesic and wet-mesic prairie; Table 3). Four models were identified as equally likely (within two AIC_c units of the best model) predictors of Henslow's Sparrow abundance (Table 3), with the best fit model including habitat and burn class without interaction effects. Two models were equally likely for Grasshopper Sparrow, with the best model including only habitat and reflecting the preference of this species for wet-mesic prairie across all burn classes (Fig. 1). The best fit model for Bachman's Sparrow also included only habitat, reflecting this species' apparent affinity for dry-mesic prairie (Fig.1), although additional models that included burn class and interaction effects were within two AIC_c units of this model.

DISCUSSION

This study determined that the number of years since fire strongly affected grassland sparrow abundance during the winter, but that relative abundance was equally, and in some cases more strongly, related to plant community type within the wet/dry mesic prairie mosaic. Each of the four sparrow taxa showed a unique response to the combination of burn year and plant community type, indicating that management and recovery strategies should maintain the heterogeneity in plant community patterns within prairie landscapes as well as heterogeneity in vegetation structure in order to provide habitat preferred both by resident and migratory birds. The federal recovery plan for the Florida Grasshopper Sparrow (USFWS 1999) focuses exclusively on habitat management for that single species and recommends a 1–3 year burn rotation. We show that co-occurring sparrows display affinities for burn rotations that, while not identical, are largely compatible with those recommended for the Florida Grasshopper Sparrow.

Management Implications by Taxon

Florida Grasshopper Sparrow.—Despite documentation of singing male Florida Grasshopper Sparrows (*A. s. floridanus*) at all sampled sites during the breeding season between the two winters in which sites were sampled in this study, individuals of this resident, federally endangered subspecies were captured in both study years only in one set of six plots in an area that has hosted a persistent breeding subpopulation at least since 1984 (Delany and Cox 1986). We could not differentiate between the two Grasshopper Sparrow subspecies in flight; therefore, Florida Grasshopper Sparrows may have been present in burn class three or four habitat but because none were captured, they were undetected by our sampling method. Based upon the low relative abundance of Florida Grasshopper Sparrows at the single location where they were captured in both years, we predict this subspecies would be in far lower abundance, if present, in burn class three or four habitat at other sites where they were undetected by our sampling method. Although we recorded small samples of the Florida Grasshopper Sparrow ($n = 5$, 2006–2007; $n = 8$, 2007–2008), we noted that individuals were flushed almost equally from both wet-mesic and dry-mesic prairie ($n = 7$, $n = 6$, respectively).

TABLE 3. Model results of plant community habitat association and burn class regressed against relative abundances of three sparrows in Florida's dry prairie. Candidate models are ranked according to Akaike's information criteria corrected for small sample size (AIC_c) for each species. Akaike weights (w_i), relative likelihood (L_i), and number of model parameters (K) are also shown.

Model	AIC_c	ΔAIC_c	w_i	L_i	K
Henslow's Sparrow					
habitat + burn	22.80	0.00	1.00	0.36	2
habitat	23.71	0.92	0.63	0.23	1
habitat*burn + habitat	23.87	1.07	0.59	0.21	2
habitat*burn + habitat + burn	23.98	1.19	0.55	0.20	3
habitat*burn	32.79	10.00	0.01	0.00	1
habitat*burn + burn	32.87	10.07	0.01	0.00	2
burn	76.80	54.01	0.00	0.00	1
Grasshopper Sparrow					
habitat	22.37	0.00	1.00	0.56	1
habitat + burn	24.42	2.04	0.36	0.20	2
habitat*burn + habitat	26.08	3.71	0.16	0.09	2
habitat*burn + habitat + burn	26.17	3.79	0.15	0.08	3
habitat*burn	28.23	5.85	0.05	0.03	1
habitat*burn + burn	28.28	5.91	0.05	0.03	2
burn	64.57	42.20	0.00	0.00	1
Bachman's Sparrow					
habitat	27.05	0.00	1.00	0.42	1
habitat + burn	28.00	0.95	0.62	0.26	2
habitat*burn + habitat	28.96	1.91	0.38	0.16	2
habitat*burn + habitat + burn	29.01	1.96	0.38	0.16	3
habitat*burn	37.64	10.59	0.01	0.00	1
habitat*burn + burn	37.67	10.62	0.00	0.00	2
burn	55.78	28.73	0.00	0.00	1

Because this sparrow must be captured for positive subspecific identification, our sampling method proved insufficient for drawing inferences about winter habitat associations.

In 2006–2007, Florida Grasshopper Sparrows were captured in burn class two prairies and in 2007–2008, those same sample plots were in burn class one condition. These burn class associations are consistent with previous research demonstrating that this resident subspecies strongly prefers burn class one and two prairie year-round and that abundance declines steeply in areas that have gone un-burned for longer than 2 years (Shriver et al. 1999, Dean 2001, Shriver and Vickery 2001, Pranty and Tucker 2006).

Regional decline in abundance of Florida Grasshopper Sparrows, juvenile dispersal, post-breeding adult dispersal, and significantly enlarged winter home ranges compared to breeding territories (Dean 2001) may explain the low detection rates observed in this study. Based on our results, we recommend that management for Florida Grasshopper Sparrows continue to emphasize fire at a frequency of 1–3 years to maintain a mosaic of vegetation structure along environmental gradients. Unfortunately, the recent and unexplained steep decline of Florida Grasshopper Sparrows across their known range with predicted extinction within a few years (Florida Grasshopper Sparrow Working Group, unpubl. data) may make our recommendation purely academic.

Grasshopper Sparrow.—Migratory Grasshopper Sparrows (*A. s. pratensis*) were found in comparable abundance in burn class one and three habitat in 2007–2008 and significantly lower abundance in burn class two, sampled in 2006–2007 (Fig. 1). Grasshopper Sparrows were least abundant in burn class four, sampled in 2006–2007. Based on the comparable abundances we detected in burn classes one and three sampled in 2007–2008, we infer that in some years Grasshopper Sparrows may be at least as abundant in burn class two. The significantly lower abundance detected in 2006–2007 in burn class two prairies may have resulted from variability in breeding success within the species' breeding range, from sampling timeframe within the winter season.

from inter-annual variation in temporal rainfall distribution at the study site with consequent prey base or vegetation density effects in the period between the 2 sample years. The Grasshopper Sparrow's preference for wet-mesic prairie habitat combined with drought conditions preceding 2006–2007 sampling may have enabled birds to occupy depression marshes and shallow sloughs, which were communities that were not sampled in this study because they normally were inundated.

Previous research on breeding Grasshopper Sparrows documented a range of relationships between breeding season abundance and time since fire. In some studies, researchers found that the sparrow was least abundant or absent in burn class one habitat and more abundant in grasslands burned two to three years prior; whereas, other studies found that Grasshopper Sparrows were most abundant in burn class one prairie with lower abundances in succeeding burn classes (Vickery 1996; USGS 2002; Powell 2006, 2008).

One previous study examined occupied breeding territory densities of Grasshopper Sparrows in relation to vegetation variables and found a strong negative relationship with woody plant cover (Ahlering 2005). Similarly, we find that overwintering Grasshopper Sparrows in Florida dry prairie have a strong affinity for graminoid and forb-dominated wet-mesic prairie devoid of woody shrubs.

In the only previous study on wintering Grasshopper Sparrows in Florida dry prairie, researchers documented that the migratory subspecies preferred burn class one prairie and recommended that dry prairie management include 2-year burn rotations. Their research also examined sparrow occupancy as a function of vegetation variables such as saw palmetto (*Serenoa repens*), forb, and litter cover but did not link the vegetation variables to dry prairie plant communities (Butler et al. 2009). In contrast, our research demonstrated that Grasshopper Sparrow abundance is linked both to fire-return interval and to plant community type. The recovery-focused fire rotations recommended for the Florida Grasshopper Sparrow (*A. s. floridanus*) will support the migrant Grasshopper Sparrow (*A. s. pratensis*) although perhaps not at optimal levels in the case of 1-year fire return intervals.

Henslow's Sparrow.—The highest abundance of Henslow's Sparrows occurred within burn class three in 2007–2008, in contrast with most of the previous winter research in which the species was most abundant within burn class one longleaf pine savannas in Louisiana, Mississippi, Alabama, and northwest Florida (Carrie et al. 2002, Tucker and Robinson 2003, Bechtoldt and Stouffer 2005, but see Palasz et al. 2010). In longleaf pine savannas, however, pine needle duff accumulates quickly, increasing the structural density of the herbaceous layer and interfering with free movement of ground-foraging sparrows. Relatively frequent fire rotations are needed to minimize litter depth and encourage herbaceous growth in longleaf pine savannas (Carrie et al. 2002). The affinity of wintering Henslow's Sparrows to the low litter accumulations in burn class one longleaf pine savannas throughout much of the species' winter range contrasts with the sparrow's preference for breeding habitat characterized by dense, tall grass and thick litter accumulations due to fire return intervals of 2 or more years (Cully and Michaels 2000; Reinking et al. 2000; Powell 2006, 2008).

In the treeless Florida dry prairie, litter accumulates differently in dry-mesic and wet-mesic communities. In the dry-mesic prairie, litter composed of saw palmetto fronds (*Serenoa repens*), oak leaves (*Quercus minima*), and other woody shrubs (e.g., *Lyonia lucida, L. fruticosa, Ilex glabra, Hypericum reductum, Bejaria racemosa*) accumulates more quickly than litter from the dead grasses and forbs in the wet-mesic prairie, which lacks woody shrubs. Therefore, wet-mesic prairie, with minimal litter accumulation (<0.5 cm; MGK, pers. obs.) in burn classes two and three, provides habitat structure for ground-foraging sparrows comparable to that in burn class one within longleaf pine savannas.

The winter 2007–2008 sampling period followed below-normal rainfall conditions during the spring and summer growing season of 2007 which may have inhibited regrowth and fruiting of cespitose grasses in burn class one prairie. The sparse vegetation may have provided inadequate cover or forage for Henslow's Sparrow; however, this inference conflicts with findings by previous researchers working in southern Louisiana, who found that maximum densities of wintering Henslow's Sparrows were predicted most accurately by low-density habitat structural characteristics rather than by seed composition or density (Johnson et al. 2011). In Florida dry prairie, however, prey abundances (seeds and arthropods) may be associated differently with burn class, habitat structure, and plant community type than

elsewhere in the species' winter range. Given the natural, historic fire return interval of ~2 years, on average, the 1–3 year rotations applied to benefit the Florida Grasshopper Sparrow will support overwintering Henslow's Sparrows in the wet-mesic prairie in burn classes two and three.

Bachman's Sparrow.—In contrast to the other three species of sparrows sampled in this study, Bachman's Sparrows strongly preferred dry-mesic prairie patches. Bachman's Sparrows predominantly occupy the understory of longleaf pine savannas and pine flatwoods in the southeastern United States, which have understory conditions similar to that of the dry-mesic patches within the Florida dry prairie (Abrahamson and Hartnett 1990, USFWS 1999). The species' affinity for treeless, dry mesic prairie at our study location is consistent with use of similar understory plant communities in longleaf pine savannas and pine flatwoods ecosystems elsewhere in the species' breeding range.

Bachman's Sparrow was most abundant in burn class one, but abundance declined progressively through burn class two, three, and four prairie, notwithstanding year effects between sample years. Our results are consistent with previous research on relative winter abundance and time since fire for this resident species (Tucker et al. 2004, 2006; Cox and Jones 2007), but this is the first study to establish this pattern in peninsular Florida. Management strategies for this species should emphasize frequent burn cycles (every 1–3 years) and the maintenance of dry-mesic grassland. Importantly, this strategy would equally benefit the endangered Florida Grasshopper Sparrow, which appears to utilize both wet and dry-mesic prairie habitats.

Across all four sparrow taxa sampled in this study, prairie plant community association and time since fire strongly affected relative abundance. Nevertheless, we found no linear relationship between sparrow abundance and plant community or burn class. The effect of time since fire on sparrow abundance is not consistent among species or across plant communities within the Florida dry prairie, and management strategies should account for these differences (Fig. 1). We recommend that land managers maintain a diversity of plant communities and burn rotations within grasslands, as suggested by our results and previously published studies, as opposed to managing exclusively for dry or wet-mesic communities and that managers continue to implement regular, 1-2 year burn cycles. Managers should also generally strive for heterogeneous burns that mimic lightning fires, as opposed to the more common homogeneous or "clean" prescribed fires, because a patchy vegetation structure promotes higher overall native species richness (Keeley et al. 2009, Myers and Harms 2011, Noss 2013). Managing for a diverse prairie landscape also may allow species to shift their habitat associations in response to the increasingly variable climate in Florida (Von Holle et al. 2010). Future research on wintering sparrows in peninsular Florida should examine associations between relative abundance of sparrows, time since fire, fire seasonality, plant community type, and winter diets across multiple years to improve understanding of winter sparrow occupancy in dry prairie and other grassland communities. Longer-term studies may reveal how sparrow-plant community associations change with annual variation in climate and provide a basis for refining predictions of winter sparrow distributions given scenarios of global climate change.

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THE IMPORTANCE OF ANTIOXIDANTS FOR AVIAN FRUIT SELECTION DURING AUTUMN MIGRATION

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ABSTRACT.—All vertebrates must contend with an increase in oxidative stress during intense exercise. Birds, in particular, may be exposed to increased oxidative stress during long-distance migration, and dietary antioxidants are likely important in alleviating the deleterious effects associated with such a stressor. We evaluated whether fruit selection by birds at a migratory stopover site in southern New England was related to the antioxidant and macronutrient content of fruits from seven commonly consumed fall-fruiting shrub species. Our objectives were to: (1) quantify, for the first time, total hydrophilic and lipophilic antioxidants, as well as two types of lipophilic antioxidants (i.e., carotenoids, and tocopherols) in wild fruits consumed by migrating birds, (2) test the hypothesis that antioxidant content of wild fruits is related to macronutrient composition, and (3) relate patterns of avian frugivory to antioxidant availability and macronutrient content of wild fruits during autumn migration. We found significant differences between fruits in total lipophilic antioxidants, carotenoids, and tocopherols, but not total hydrophilic antioxidants. *Viburnum* spp. and *Myrica pennsylvanica* had the most lipophilic antioxidants and tocopherols, whereas *Celastrus orbiculatus* and *Rosa multiflora* contained the most carotenoids. Carotenoid content was positively correlated with protein content but no significant relationships were evident between the other antioxidants and macronutrients. Fruit consumption was negatively correlated with carotenoid content and was not related to any other antioxidant measure. Interestingly, the most consumed fruit species, arrowwood, was among the highest in fat, total lipophilic antioxidants, and tocopherols. These data indicate that antioxidant content differs significantly between fruit species and suggest that (1) birds can acquire different types of antioxidants depending on the fruits they select and (2) lipophilic antioxidants, especially tocopherols, may be important antioxidants for birds during autumn migration. *Received 17 January 2013. Accepted 19 April 2013.*

Key words: antioxidant, carotenoid, fruit preference, migratory birds, tocopherol.

All aerobic organisms produce reactive oxygen species (ROS) as unavoidable byproducts of respiration and an over-production of these reactive species is associated with damage to key physiological systems (Barja 2000, Wiersma et al. 2004, Halliwell and Gutteridge 2007, Costantini 2008). Birds may be exposed to especially high levels of ROS production as a consequence of long-duration flight (Costantini et al. 2007, 2008). Birds and other vertebrates have evolved several mechanisms to cope with this oxidative burden, including an ability to increase endogenous antioxidant production (e.g., uric acid and enzymatic antioxidants) (Balaban et al. 2005, Tsahar et al. 2006, Costantini 2008, Monaghan et al. 2009) and to preferentially consume and metabolize dietary antioxidants (e.g., carotenoids, tocopherols, and polyphenolic compounds) (Catoni et al. 2008a, Costantini 2008, Monaghan et al. 2009). Currently, little is known about where birds might acquire specific antioxidants in their diet, because the antioxidant composition of wild foods is not yet well established (Schaefer et al. 2003, 2008; Hill and McGraw 2006).

During autumn migration, many birds that are primarily insectivorous during the summer months switch to eating seasonally-abundant fruits (Thompson and Willson 1979, Herrera 1984, Parrish 1997, Klasing 1998, McWilliams et al. 2004). Many of these fruits may be excellent sources of dietary antioxidants and could provide an important defense against oxidative stress for both fruiting plants and their consumers (Garcia-Alonso et al. 2004; Smith et al. 2007; Catoni et al. 2008a, b; Bolser et al. 2013). Most antioxidants in fruits can be classified either as lipophilic (e.g., carotenoids and tocopherols) or hydrophilic (e.g., ascorbic acid and polyphenolic compounds) (Crozier et al. 2006, Catoni et al. 2008b, Costantini 2008). Despite the potential importance of lipophilic antioxidants to health, very few studies have directly measured their concentration in fruits. Schaefer et al. (2008) measured the carotenoid content of 60 wild fruit species commonly consumed by birds and found that *Tamus communis*, *Streptopus amplexifolius*, *Polygonatum multiflorum*, and *Rosa glauca* had the

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highest amounts. Considerably more attention has been given to hydrophilic antioxidants and several studies have specifically measured these antioxidants in fruits. Benvenuti et al. (2004) observed high hydrophilic antioxidant activity in fruits from the genera *Rubus, Ribes,* and *Aronia.* Schaefer et al. (2008) found that fruits from American elderberry (*Sambucus canadensis*), black mulberry (*Morus nigra*), burnet rose (*Rosa pimpinellifolia*), common dogwood (*Cornus sanguinea*), and hawthorne (*Crataegus* spp.) contained the most anthocyanins of 60 plant species they studied. More recently, Bolser et al. (2013) quantified hydrophilic antioxidants in fruits from seven shrub species at a southern New England stopover site and found that arrowwood (*Viburnum* spp.) fruits contained high levels of anthocyanins and other phenolics, whereas fruits from multiflora rose (*Rosa multiflora*), Asiatic bittersweet (*Celastrus obiculatus*), and winterberry (*Ilex verticillata*) contained virtually none of these antioxidants. No previous studies have quantified both the lipophilic and hydrophilic antioxidant content of wild fruits nor have they related such measures to fruit selection by wild birds.

To date, no studies have specifically investigated the relationship between the macronutrient content and antioxidant content of wild fruits consumed by free-living birds. In both natural and processed foods, the susceptibility of lipids to oxidation is a major cause of quality deterioration (Frankel 1996). One of the most effective means of retarding lipid oxidation in fatty foods is through antioxidant protection (Decker 1998a, b; Frankel 1996; Reisch et al. 1998). Specifically, lipophilic antioxidants extracted from plants (e.g., tocopherols) are especially potent in preventing oxidation in food emulsions (McClements and Decker 2000). A direct correlation has been established between the polarity of antioxidants and their effectiveness in inhibiting oxidation. Highly polar antioxidants (e.g., hydrophilic antioxidants) are much less efficient in inhibiting lipid oxidation than non-polar antioxidants (e.g., lipophilic antioxidants) (Schwarz et al. 1996), because hydrophilic antioxidants are located primarily in aqueous phases, away from where lipid oxidation occurs, whereas lipophilic antioxidants are located both in fatty tissues and in the lipid membranes of cells where the bulk of lipid oxidation occurs (McClements and Decker 2000). As such, it is possible that plants with high-fat fruits (e.g., arrowwood; Smith et al. 2007) may allocate more antioxidants, particularly lipophilic antioxidants, to these fruits to protect against oxidative damage, though this relationship has yet to be directly demonstrated.

The influence of antioxidant levels on avian fruit selection has only recently received attention from ornithologists. α-tocopherol, a form of vitamin E, is commonly used as a supplement to improve broiler chicken health and quality (Marusich et al. 1975, Boa-Amponsem et al. 2000, Leshchinsky and Klasing 2001, Surai 2002) and carotenoids are well-known contributors to plumage coloration and sexual signaling in several bird species (Olsen and Owens 1998, Hill 2000, Hill et al. 2002, Shawkey et al. 2006). Although lipophilic antioxidants provide these nutritional benefits, the influence of tocopherols on avian food preference has yet to be investigated. A few studies have directly assessed how carotenoids influence food selection by birds, although these have produced contradictory results. For example, Senar et al. (2010) found that Great Tits (*Parus major)* consistently chose carotenoid-enriched mealworms over non-enriched mealworms; however, male Society Finches (*Lonchura domestica)* offered a carotenoid-enriched diet did not consume more food than birds offered a non-enriched diet (McGraw et al. 2006) and Garden Warblers (*Sylvia borin)* did not preferentially consume carotenoids when offered a choice between cartenoid-supplemented and non-supplemented food (Catoni et al. 2011). Hydrophilic antioxidants, on the other hand, have been widely used in behavioral diet choice trials. Schaefer et al. (2008) found that Eurasian Blackcaps (*Sylvia atricapilla*) preferred artificial diets supplemented with anthocyanins over foods without these supplements, and Catoni et al. (2008a) showed that Eurasian Blackcaps preferred food with flavonoids over food without flavonoids. In addition, free-living birds selected arrowwood fruits containing more anthocyanins over lower-anthocyanin fruits from other fruiting-shrub species during autumn migration (Bolser et al. 2013).

No previous studies have determined the extent to which free-living birds select wild fruits based on their specific hydrophilic and lipophilic antioxidant content. In this study, we evaluated whether fruit selection by birds at an important stopover site in southern New England was related to the antioxidant and macronutrient content of wild fruits from seven fall-fruiting

shrub species. Our specific objectives were to: (1) quantify total hydrophilic and lipophilic antioxidants, as well as two types of lipophilic antioxidants (i.e., carotenoids, and tocopherols) in wild fruits consumed by migrating birds, (2) test the hypothesis that antioxidant content of wild fruits is related to macronutrient composition, and (3) relate patterns of avian frugivory to antioxidant availability and macronutrient content of wild fruits during autumn migration.

METHODS

Study Area and Bird Species Composition.—Fieldwork was conducted on Block Island, Rhode Island (41° 13′ N, 71° 33′ W), an island located 15.5 km south of Rhode Island's coast and 22.5 km northeast of Long Island, New York, USA. The study site was located on the northeast portion of the island, within the Bay Rose and Clay Head preserves, where migratory birds are known to concentrate and fall-fruiting shrub species are abundant (Able 1977; Parrish 1997, 2000; Hammond 2002; Reinert et al. 2002; Comings 2005; Smith et al. 2007; Smith and McWilliams 2010). The site itself was 27 ha in size and was bounded by Corn Neck Road to the west, Mansion Road to the south, the coast to the east, and Kurz Road to the north. The majority of the site can be classified as maritime shrubland habitat with salt spray and wind disturbance as the primary determinants of plant species composition (Hammond 2002). Exposed areas were dominated by northern bayberry (*Myrica pensylvanica*), eastern poison ivy (*Toxico dendronradicans*), and downy goldenrod (*Solidago puberula*); whereas areas that were more sheltered supported arrowwood, chokeberry (*Aronia* sp.), and Virginia creeper (*Parthenocissus quinquefolia*). Two nonnative species, Asiatic bittersweet and multiflora rose, were also abundant throughout the study site.

During fall migration, approximately 113 different bird species are known to stopover on Block Island (Reinert et al. 2002). The three most abundant bird taxa are warblers, mimic-thrushes, and New World sparrows. Within these taxa, the most common species include the Yellow-rumped Warbler (*Setophaga coronata*), Gray Catbird (*Dumetella carolinensis*), Golden-crowned Kinglet (*Regulus satrapa*), and Red-eyed Vireo (*Vireo olivaceus*) (Reinert et al. 2002). Average stopover length of songbirds on Block Island differs between species and has been estimated to range from a mean (± SD) of 2.57 ± 2.51 days in Golden-crowned Kinglets to 7.17 ± 6.42 days in Ovenbirds (*Seiurus aurocapilla*; Parrish 1997).

Fruit Collection and Consumption Data.—Avian fruit consumption was measured in a previous study (Bolser et al. 2013) from September–November 2009 at seven randomly chosen locations on Block Island. During this time, seven fall-fruiting shrub species were assessed for consumption rate and included: arrowwood, northern bayberry, Asiatic bittersweet, chokeberry, multiflora rose, Virginia creeper, and winterberry. Study locations were chosen by overlaying the study site with a numbered grid consisting of 300 × 300 m cells and randomly choosing cells within the grid. Locations were accepted if they contained at least one fruiting plant of each of the seven species within 150 m of the center of a selected grid cell. When a given location included more than one fruiting plant, we chose to sample fruits from the nearest plant to the central point that had a pair of branches with at least 25 fruits per branch. One branch on the selected plant was enclosed with thin-plastic mesh (0.5-cm grid) that prevented birds but not most invertebrates from accessing the fruits (more detailed description of these methods provided by Smith et al. 2007). A partner branch was marked and remained uncovered. Only nine terrestrial mammal species occur on Block Island, none of which are known to commonly consume fruits (Lang and Comings 2001). Thus, songbirds are the primary consumers of fruits on Block Island during fall, and the majority of these birds are stopping over during migration. The number of fruits on each marked branch was counted during the primary fall songbird migration beginning in early September and every 7–14 days thereafter for a total of five counts. The procedure involved repeated counting of the number of fruits on each branch until a consistent number was attained (Bolser et al. 2013).

We collected fruit samples at peak ripeness from the same seven plant species and locations during September–October 2011. Arrowwood, bayberry, and chokeberry were collected from early to mid September, winterberry and Virginia creeper were harvested from late September through early October, and bittersweet and multiflora rose were collected from mid through late October. All samples were stored at −80 °C until analysis.

Sample Preparation and Antioxidant Extraction.—Between 10–15 g of fruit were manually

deseeded per sample and the resulting skin and pulp stored at −80 °C until analysis. Both total hydrophilic and total lipophilic antioxidants were extracted using procedures detailed by Thaipong et al. (2006). Briefly, total hydrophilic antioxidants were extracted by homogenizing 3 g fresh weight of deseeded skin and pulp in 25 mL of methanol using a Waring Blender (Waring Laboratory Science, Torring, CT) and allowing the homogenate to saponify for 12 hrs at 4 °C. Following saponification, the homogenate was spun at 6,825 RPM in a tabletop centrifuge (Allegra 21R, Beckman Coulter, Brea, CA) at 4 °C for 20 mins. The supernatant was then recovered and stored at −80 °C for later analysis. Total lipophilic antioxidants were extracted by homogenizing the leftover pellet with 20 mL of dichloromethane. The homogenate was then immediately centrifuged at 6,925 RPM at 4 °C for 20 mins, and the resulting supernatant was recovered and stored until analysis.

To extract tocopherols and carotenoids, fruit samples were weighed in 1.5 mL screw-cap microtubes to the nearest 0.01 mg and ground for 20 mins at 30 Hz using a ball mill (MM200, Retsch GmbH & Co. KG, Haan, Germany) in the presence of 1 mL hexane:methyltert butyl (1:1, v/v) and steel grinding balls (Toomey and McGraw 2010). The samples were then centrifuged for 3 mins at 10,000 RPM, after which time the supernatant was transferred to a fresh tube and evaporated to dryness under a stream of nitrogen.

Chemical Analysis of Extracts.—All of the fruit samples were assessed for concentrations of: (1) total hydrophilic antioxidants, (2) total lipophilic antioxidants, (3) composite antioxidants, (4) tocopherols, and (5) carotenoids. Various measures have been used to assess antioxidant status in biological samples, the advantages and disadvantages of which have been extensively reviewed and discussed (Prior and Cao 1999, Sanchez-Moreno 2002, Schlesier et al. 2002, Haung et al. 2005, Ozgen et al. 2006, Thaipong et al. 2006, Halliwell and Gutteridge 2007). We chose to use a modified DPPH (2,2-Diphenyl-1-picrylhydrazyl) spectrophotometric procedure, as detailed by Thaipong et al. (2006), to measure total hydrophilic and total lipophilic antioxidants and we further adjusted this protocol for analysis using 96-well microplates and a microplate spectrophotometer. Briefly, a DPPH stock solution was prepared by dissolving 0.024 g of DPPH in 50 mL of methanol and a working DPPH solution was subsequently prepared by adding 18 mL of the DPPH stock to 32 mL of methanol to yield an approximate absorbance of 1.5 at 515 nm. Trolox (6-hydroxy-2,5,7,8-tetramethylchroman-2-carboxylic acid), a vitamin E analog, was used to construct a standard curve linear between 25 and 1,500 µM. 25 µL of either standard or sample were reacted with 475 µL of DPPH working solution under dark conditions for 24 hrs in 1.7 mL polypropylene microcentrifuge tubes. Following this 24-hr period, 300 µL of reacted sample or standard were pipetted into the wells of a 96-well microplate and the absorbance read at 515 nm in a microplate spectrophotometer (PowerWave 340, Bio-Tex, Winooski, VT). A standard curve was constructed by plotting the absorbance of the Trolox standards against their corresponding concentrations and the resulting regression equation was used to calculate the sample antioxidant concentrations. The DPPH protocol was performed twice for each fruit sample, once using the total hydrophilic extracts and once using the total lipophilic extracts, so that we could obtain separate measures for total hydrophilic and total lipophilic antioxidants. Composite antioxidant concentration was calculated by adding the total hydrophilic and total lipophilic antioxidant concentrations together for each sample. Total hydrophilic and lipophilic antioxidants were measured at the University of Rhode Island (Kingston, RI). All chemicals and reagents were purchased through Sigma-Aldrich Chemical Corporation (St. Louis, MO).

Carotenoids and tocopherols were analyzed at Arizona State University (Tempe, AZ) using spectrophotometric protocols as described by Toomey and McGraw (2010). Briefly, fruit extracts were resuspended in 1 mL hexane:MTBE (1:1, v/v) and transferred to a clean quartz cuvette for measurement with an absorbance spectrophotometer. Absorbance data were gathered at 450 nm for carotenoids and 301 nm for tocopherols. The extinction coefficients for calculating concentrations of carotenoids (Clotfelter et al. 2007) and tocopherols (Budvari 1989) were 2,550 and 3,270 respectively.

Statistical Analysis.—We assessed the Pearson's Product Moment Correlations between each of the five dependent variables (total hydrophilic antioxidants, total lipophilic antioxidants, composite antioxidants, tocopherols, and carotenoids) to investigate the relationships between the different classes of antioxidants. Total lipoph-

TABLE 1. Pearson's Product Moment Correlations for amounts of five different measures of antioxidants in fruits from seven fall-fruiting shrub species on Block Island, Rhode Island, in southern New England. Significant correlations are denoted by bolded text.

	Total hydrophilic	Total lipophilic	Composite antioxidants	Carotenoids
Total Lipophilic				
$r =$	−0.087	—	—	—
$P =$	0.58			
Composite Antioxidants				
$r =$	0.208	0.956	—	—
$P =$	0.18	**<0.0001**		
Carotenoids				
$r =$	0.177	−0.024	0.029	—
$P =$	0.26	0.88	0.86	
Tocopherols				
$r =$	−0.147	0.336	0.287	0.307
$P =$	0.34	**0.03**	**0.06**	**0.05**

and composite antioxidants exhibited an almost perfect correlation with one another (Table 1) suggesting that lipophilic antioxidants were responsible for driving composite antioxidant values. As such, we dropped composite antioxidants from the remaining statistical analyses. We constructed separate One-Way ANOVA models for each of the four remaining dependent variables to determine whether there were significant differences in antioxidants between fruit species. One-Way ANOVA models were also constructed to assess differences in three macronutrient measures (i.e., fat, carbohydrate, protein; Smith et al. 2007) between fruit species. Post-hoc Tukey's HSD Multiple Comparisons Analyses were performed to compare nutrient differences between each pair of fruit species for three antioxidant metrics (total lipophilic antioxidants, carotenoids, and tocopherols) and for the three macronutrient metrics. Total hydrophilic antioxidants were excluded from these comparisons as we did not find any overall significant differences between fruit species.

We performed an additional Pearson's Product Moment Correlations analysis to assess the relationship between macronutrient and antioxidant content of the seven plant species. We compared the average fat, protein, and carbohydrate content (from Smith et al. 2007) for each plant species to the average values of the four antioxidant metrics that we measured. To assess the relationship between avian fruit consumption, antioxidant content, and macronutrient content, we performed a Spearman's Rho Correlation analysis using ranked consumption data (from Bolser et al. 2013). The plant species with the lowest consumption index was ranked 1 and the plant species with the highest was ranked 7. For each antioxidant and macronutrient metric, we used the average rank for each plant species whenever there were non-significant differences between specific plant species as indicated by our multiple comparisons analyses. We did not include total hydrophilic antioxidants in this analysis because we found no overall differences in these antioxidants between plant species.

All statistical analyses were performed using SAS 9.2 statistical software (SAS Institute 2009) and results were considered significant at the $\alpha = 0.05$ level.

RESULTS

There was an exceptionally strong positive correlation between total lipophilic and composite antioxidants and moderate, but significant, positive correlations between total lipophilic antioxidants and tocopherols and between tocopherols and carotenoids (Table 1). The results of our One-Way ANOVA models indicated that there were significant differences in lipophilic antioxidants ($F_{6,36} = 32.65$, $P < 0.001$; Fig. 1A), carotenoids ($F_{6,36} = 33.15$, $P < 0.001$; Fig. 1B), and tocopherols ($F_{3,36} = 6.86$, $P < 0.001$; Fig. 1B) in fruits from the seven shrub species and no significant differences in total hydrophilic antioxidant content ($F_{6,36} = 1.71$, $P = 0.15$; Fig. 1B).

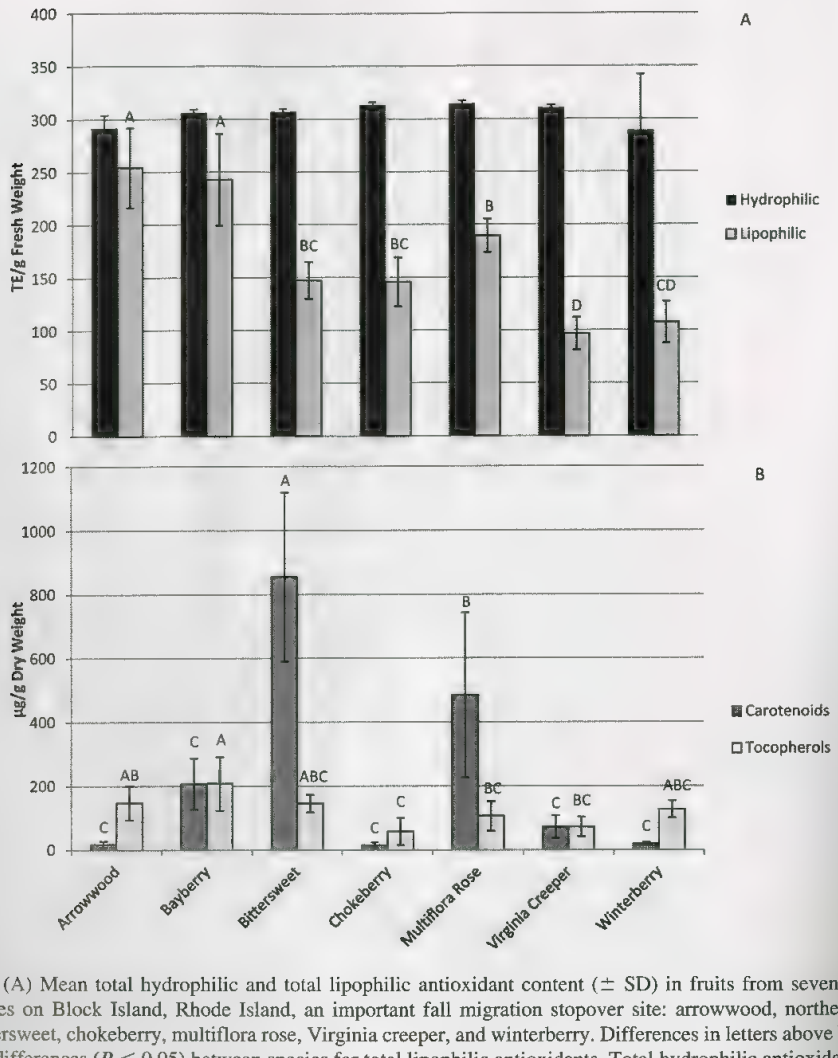

FIG. 1. (A) Mean total hydrophilic and total lipophilic antioxidant content (± SD) in fruits from seven fall-fruiting shrub species on Block Island, Rhode Island, an important fall migration stopover site: arrowwood, northern bayberry, Asiatic bittersweet, chokeberry, multiflora rose, Virginia creeper, and winterberry. Differences in letters above bars indicate significant differences ($P < 0.05$) between species for total lipophilic antioxidants. Total hydrophilic antioxidants were not significantly different among species. (B) Mean carotenoid and tocopherol content (± SD) in fruits from the same seven plant species. Differences in letters above bars indicate significant differences ($P < 0.05$) between species for a given antioxidant.

Total lipophilic antioxidants were highest in fruits from arrowwood and bayberry, moderately high in multiflora rose, bittersweet, chokeberry, and winterberry, and lowest in Virginia creeper (Fig. 1A). Carotenoids were much higher in fruits from bittersweet and multiflora rose than in any of the other shrub species, whereas tocopherols were highest in fruits from bayberry and arrowwood, moderately high in bittersweet, winterberry, multiflora rose, and Virginia creeper, and lowest in chokeberry (Fig. 1B).

We found no significant correlations between any of our fruit antioxidant metrics and macronutrient content except for a fairly strong positive relationship between protein and carotenoids in fruits (Table 2). Consumption rank was negatively correlated with carotenoid rank (carotenoids: $r_s = -0.76$, $P = 0.05$) but was not correlated with either of the other ranked antioxidant metrics (total lipophilic antioxidants: $r_s = 0.036$, $P = 0.94$; tocopherols: $r_s = 0.36$, $P = 0.42$) or with ranked macronutrient content (fat: $r_s = 0.61$,

TABLE 2. Pearson's Product Moment Correlations for antioxidant and macronutrient content of fruits from seven fall-fruiting shrub species on Block Island, Rhode Island, in southern New England. Significant correlations are denoted by bolded text.

Type of antioxidant	Type of macronutrient		
	Fat	Protein	Carbohydrate
Total Hydrophilic			
$r =$	−0.260	0.505	0.250
$P =$	0.57	0.25	0.59
Total Lipophilic			
$r =$	0.677	−0.393	−0.688
$P =$	0.09	0.38	0.09
Carotenoids			
$r =$	−0.337	0.840	0.327
$P =$	0.46	**0.02**	0.47
Tocopherols			
$r =$	0.632	−0.171	−0.632
$P =$	0.13	0.71	0.13

= 0.15; protein: $r_s = -0.655$, $P = 0.11$; carbohydrate: $r_s = -0.611$, $P = 0.15$) (Fig. 2).

DISCUSSION

Antioxidant and Macronutrient Content of Wild Fruits.—Antioxidants in fruits are secondary metabolites that plants may synthesize to protect themselves against the oxidative stress brought about by lipid metabolism (Catoni et al. 2008a). Specifically, lipophilic antioxidants extracted from plants (e.g., tocopherols) are especially potent in preventing oxidation in natural and processed foods (Decker 1998a, b; Frankel 1996; Reisch et al. 1998; McClements and Decker 2000). As such, plants that produce high-fat fruits may allocate more lipophilic antioxidants to these fruits to protect against oxidative damage. Consistent with this hypothesis, arrowwood and bayberry fruits had the highest fat content of the seven plant species (Smith et al. 2007) and they contained the highest concentrations of total lipophilic antioxidants (Fig. 1A). In contrast, Virginia creeper fruits were also high in fat, yet they contained some of the lowest concentrations of total lipophilic antioxidants (Fig. 1A). This is especially surprising considering that Virginia creeper fruits are comprised primarily of 18:2 polyunsaturated fatty acids (PUFA; Boyles 2011) (fatty acid nomenclature = C:D, where C = the number of carbons and D = the number of double bonds), which are much more susceptible to oxidative attack than either monounsaturated fatty acids (MUFA) or saturated fatty acids (Klasing 1998, Hulbert 2007). Arrowwood fruits are comprised mostly of 16:1 and 18:1 MUFA and bayberry fruits contain mostly 16:0 and 18:0 saturated fatty acids (Boyles 2011). As such, the benefit of fruit antioxidants for these plants may be related more to the quantity rather than the composition of the fats in these fruits. In general, antioxidant protection may not always be the main function of lipophilic antioxidants in fruits. For example, secondary metabolites (e.g., antioxidants) may function as attractants for seed dispersers by signaling a nutritional reward (Cipollini and Levey 1997a). In this case, arrowwood and bayberry shrubs might produce high-antioxidant fruits with more anthocyanins (Bolser et al. 2013) as a strategy by which to attract migratory songbirds that require dietary antioxidants to meet their nutritional needs during stopover. In addition, all of the fruits we studied contained high levels of total hydrophilic antioxidants, which may be sufficiently effective at mitigating oxidative damage without the additional protection of lipophilic antioxidants. In fact, Bolser et al. (2013) measured hydrophilic antioxidants in fruits from the same seven shrub-species and found that Virginia creeper fruits had among the highest phenolic content.

We also detected significant differences in carotenoids between the seven fall-fruiting shrubs we studied. Bittersweet and multiflora rose fruits had exceptionally high levels of carotenoids in comparison to all of the other shrub species (Fig. 1B) and also contained the highest protein concentrations (Table 2) (Smith et al. 2007). Virginia creeper fruits contained very few carotenoids (Fig. 1B), but they were also high in protein (Smith et al. 2007). Both bittersweet and multiflora rose fruits are bright red in color when ripe and this hue is well known to be associated with the presence of carotenoids, such as canthaxanthin (Bartley and Scolnik 1995, Hill 2000). Interestingly, winterberry also produces bright red fruits but had relatively low amounts of carotenoids. In general, little evidence has been found in support of a direct association between fruit color and nutrient content (Willson and Whelan 1990, Schaefer et al. 2008), though birds have been shown to exhibit a foraging preference for both red-hued food sources (Stockton-Shields 1997) and purple-hued food sources (Zhang et al.

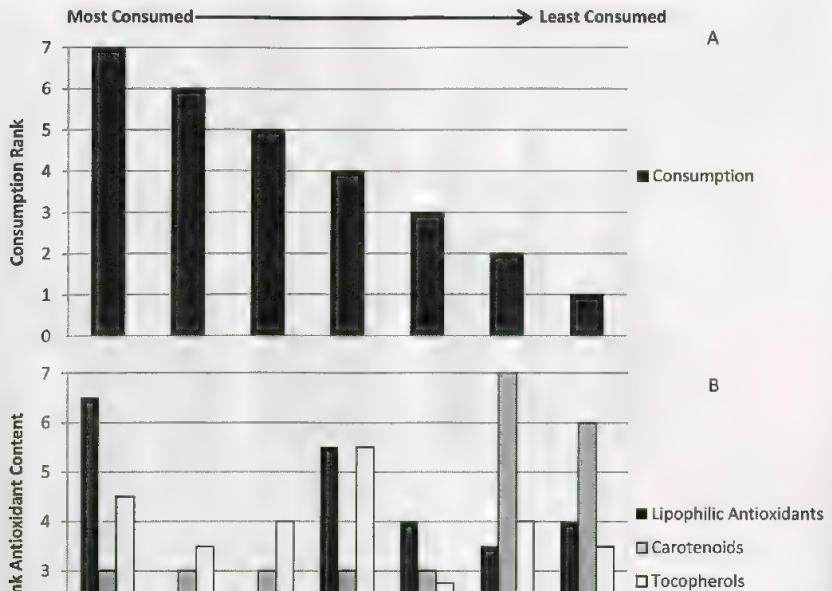

FIG. 2. (A) Rank order in which songbirds during fall migration on Block Island, Rhode Island, consumed fruits fr seven fall-fruiting shrub species including: arrowwood, Virginia creeper, winterberry, northern bayberry, chokeberr Asiatic bittersweet, and multiflora rose. Note that a higher rank indicates higher consumption (e.g., arrowwood w consumed most commonly of the seven species). (B) Mean rank antioxidant content including total lipophilic antioxidan carotenoids, and tocopherols in fruits from the seven shrub species. Total hydrophilic antioxidants were excluded beca they were not significantly different between fruit species. (C) Mean rank macronutrient content including fat, protein, a carbohydrate in fruits from the seven shrub species.

2012). In addition, low-quality fruits may mimic the color of high-quality fruits as a way to attract seed dispersers without investing energy in producing high-cost fruits (Cipollini and Levey 1997a).

The pattern of tocopherol abundance in fru was similar to that of total lipophilic antioxida but different than that of carotenoids, the oth specific class of lipophilic antioxidants that measured. Specifically, tocopherols were high

in fruits from both bayberry and arrowwood, moderate in bittersweet, winterberry, multiflora rose, and Virginia creeper and lowest in chokeberry (Fig. 2–1B). The high fat content of bayberry and arrowwood fruits may contribute to high concentrations of lipophilic antioxidants, such as tocopherols, in their pulp. α-tocopherol is well-documented as a potent antioxidant for improving immune function and mitigating oxidative damage in broiler chickens (Marusich et al. 1975, Boa-Amponsem et al. 2000, Leshchinsky and Klasing 2001, Surai 2002) and may provide similar benefits to free-living birds. If wild songbirds require such antioxidants to mitigate oxidative damage during migration, it is possible that the tocopherols in wild fruits may act as attractants for seed dispersers.

Total hydrophilic antioxidants were not different between fruit species and this finding is in disagreement with the findings of a similar study that found significantly higher levels of two specific hydrophilic antioxidants, phenolics and anthocyanins, in arrowwood fruits than in fruits from other shrub species on Block Island (Bolser et al. 2013). This apparent contradiction likely reflects the fact that our measure of hydrophilic antioxidants was more general than those used by Bolser et al. (2013). Songbirds differentiate between diets that differ in anthocyanins in both controlled studies (Schaefer et al. 2008) and in field studies (Bolser et al. 2013), suggesting that the amounts of specific types of hydrophilic antioxidants (e.g., anthocyanins, phenolics, flavonoids) in fruits and other foods may be more relevant than total hydrophilic antioxidant content alone.

In assessing the relationships between different classes of antioxidants, we expected to find significant correlations between total lipophilic antioxidants, carotenoids, and tocopherols given that the latter two are a subset of the former. We found significant positive relationships between total lipophilic antioxidants and tocopherols and between tocopherols and carotenoids (Table 1); however, no such relationship was evident between total lipophilic antioxidants and carotenoids. The two fruits highest in carotenoid content, bittersweet and multiflora rose, only contained moderate amounts of total lipophilic antioxidants and the two fruits with the highest total lipophilic antioxidants, arrowwood and bittersweet, contained some of the lowest carotenoid concentrations. Of the fruits that had the highest total lipophilic antioxidants, tocopherols made up the majority of those lipophilic antioxidants, whereas carotenoids were fairly minor contributors (Fig. 1). This may indicate that tocopherols are the more important lipophilic antioxidants during autumn migration, both for plants and their consumers, at least in these fall-fruiting shrub species in southern New England.

The relative amounts of antioxidants that we found in wild fruits in southern New England were similar to those reported in the few other studies that have quantified the antioxidant content of commercial and wild fruits. Wu et al. (2004) quantified the total hydrophilic and total lipophilic antioxidant capacities of common United States foods and found that, of the fruits they measured, Haas avocado (*Persea americana*), a high fat fruit, had exceptionally high amounts of lipophilic antioxidants. Other fruits with high concentrations of lipophilic antioxidants included cranberry (*Vaccinium macrocarpon*), raspberry (*Rubus* spp.), and shrubby blackberry (*Rubus fruticosus*), though these levels were considerably lower than those of avocado. Cranberry and blackberry fruits also had very high concentrations of hydrophilic antioxidants. Schaefer et al. (2008) measured carotenoids in fruits commonly consumed by birds and found that fruits from *Streptopus amplexifolius, Polygonatum multiflorum, Tamus communis,* and *Rosa glauca* contained the highest amounts. They also found low levels of carotenoids in fruits from Virginia creeper, which is in agreement with our results. Lastly, Chun et al. (2006) measured total tocopherol content in raw and processed fruits and vegetables and found that green olives (*Olea europaea*), which are high in fat, contained the most tocopherols followed closely by blackberry and raspberry. The findings of these studies, along with our own, support the hypotheses that: (1) high fat fruits often also contain high levels of lipophilic antioxidants, though there are many exceptions, and (2) many fruits are good sources of both hydrophilic and lipophilic antioxidants. Our results demonstrate for the first time that the relationships between the amounts of different types of antioxidants and macronutrients are complex and that consumers cannot eat only one or a few fruit types to satisfy their nutritional requirements.

Antioxidants and Fruit Consumption.—We expected birds to consume fruits with higher antioxidant content at a higher rate than fruits with lower amounts of antioxidants since these dietary antioxidants may act to mitigate the

negative effects of oxidative stress (Garcia-Alonso et al. 2004; Catoni et al. 2008a, b; Costantini 2008, Monaghan et al. 2009). We found that the most highly consumed fruit species, arrowwood, also had among the highest fat content, highest total lipophilic antioxidants, and highest tocopherols of the seven shrub species (Fig. 2). The second most consumed species, Virginia creeper, also had high fat content (Smith et al. 2007). Interestingly, the least consumed species (chokeberry, bittersweet, and multiflora rose) were lowest in fat, highest in carbohydrate, and among the lowest in both total lipophilic antioxidants and tocopherols (Fig. 2). There was also a significant negative relationship between fruit consumption and carotenoid content (Table 2), because two of the least consumed fruits, bittersweet and multiflora rose, were exceptionally high in carotenoids. Other studies of birds have suggested that the antioxidant benefits derived from carotenoid consumption are meager (Costantini and Møller 2008, Simons et al. 2012) and thus support the hypothesis that other types of antioxidants, such as tocopherols, are more important for protecting against oxidative damage. Bolser et al. (2013) measured two specific types of hydrophilic antioxidants, phenolics and anthocyanins, in fruits from these same seven fall-fruiting species on Block Island and found that arrowwood fruits had the highest amounts. Interestingly, recent studies have suggested that the absorption of dietary antioxidants may be improved by concomitant consumption of dietary fat (Pietta 2000, Prior 2003). This may explain why high-fat fruits with high antioxidant content may be preferentially consumed over fruits with less fat and low antioxidant content. The trends we observed suggest that birds on Block Island during fall migration select high-fat fruits and might also select fruits based on high antioxidant content in order to meet their nutritional needs during stopover.

Multiple factors influence patterns of avian fruit selection and this likely explains why we found no significant correlation between consumption rank and the relative amounts of antioxidants that we measured in our study. Studies of both wild and captive songbirds have shown that fruit preference can be influenced by fat content (Stiles 1993, Fuentes 1994), sugar content (Levey 1987, Lepczyk et al. 2000), specific amino acids (Parrish and Martin 1977), fatty acids (McWilliams et al. 2002, Pierce et al. 2004), fruit color (Willson et al. 1990, Puckey et al. 1996), and pulp-to-seed ratio (Sorenson 1984, Izhaki 1992, Murray et al. 1993, Stanley and Lill 2002). In addition, birds may diversify their diet to avoid consuming toxic levels of particular secondary chemical compounds (Barnea et al. 1993; Cipollini and Levey 1997a, b; Levey and Cipollini 1998; Schaefer et al. 2003). Abundance and distribution of plant species in the environment may also contribute to the fruit selection patterns of wild birds (Baird 1980, Moermond and Denslow 1983, Sargent 1990, Whelan and Willson 1994). For example, arrowwood is one of the most abundant fruiting plant species on Block Island while other fruits, such as Virginia creeper, are much less abundant, not nearly as widely distributed, and are thus less available to birds during stopover (Smith et al. 2007). Unlike controlled laboratory or captive bird studies where single factors can be manipulated, field studies such as ours can, at best, detect general trends in bird biology and behavior. Though multiple factors may influence patterns of avian frugivory, the results of our study demonstrate that there are significant differences in antioxidant content between fruit species and, therefore, birds may be capable of altering the amounts and types of dietary antioxidants they consume based on the fruits they select. The trends we observed suggest that birds on Block Island during fall migration tend to select high-fat fruits, such as arrowwood, and that these fruits also contain high levels of total lipophilic antioxidants and tocopherols, in particular. Given these trends, it is possible that lipophilic antioxidants, particularly tocopherols, are especially important for birds and may influence patterns of frugivory at stopover during autumn migration.

CONCLUSIONS

The results of our study provide novel insights into the specific antioxidant content of wild fruits that are commonly consumed by free-living migratory songbirds during autumn migration. Our study is the first to measure total lipophilic antioxidants and total hydrophilic antioxidants in wild fruits on Block Island and to relate antioxidant content to both macronutrient composition and fruit consumption by free-living birds. Future research should investigate the food preferences of captive birds for specific macronutrients and antioxidants (e.g., tocopherols and carotenoids) using controlled diet choice trials. Such studies should supplement semi-synthetic diets with high levels of these antioxidants and vary macronutrient content to determine the different antioxidant/macronutrient combinat

interact to influence the dietary preferences of captive birds. Understanding the nutritional requirements of songbirds during autumn migration is complex but essential for the effective management of bird habitats at stopover. Better knowledge about wild songbird nutrition and feeding behavior will allow conservationists to manage important stopover sites for preferred fruit species and will ultimately increase the value of such sites to the migrants that use them.

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FOOD AVAILABILITY IN EXOTIC GRASSLANDS: A POTENTIAL MECHANISM FOR DEPAUPERATE BREEDING ASSEMBLAGES

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ABSTRACT.—We investigated the influence of Old World bluestem (*Bothriochloa ischaemum*; OWB) monocultures on grassland bird abundance through analysis of vegetation structure and food availability. We compared breeding bird density, vegetation structure and composition, and arthropod biomass between six native grass and six OWB fields in the southern Great Plains. The OWB fields supported 1.70 ± 0.27 (mean ± SE) Grasshopper Sparrows (*Ammodramus savannarum*) per ha compared to 0.95 ± 0.25 in native grass fields, but total species richness was greater in native grass fields (40 versus 28 species). Density of some bird species was correlated with vegetation structure regardless of field type, suggesting that management practices may be more influential than plant species composition. Mean arthropod biomass was 3.39× greater in native grass fields than in OWB monocultures. Native grass fields provided habitat for a larger complement of birds than did OWB monocultures, and reduced food availability in OWB fields suggests a mechanism for that difference. *Received 3 January 2013. Accepted 7 April 2013.*

Key words: arthropod biomass, *Bothriochloa ischaemum*, Conservation Reserve Program, grassland birds, invasive species, mixed-grass prairie, Old World bluestem.

Grassland bird populations have declined rapidly across North America (Peterjohn and Sauer 1999, Sauer et al. 2008), with habitat loss, degradation, and fragmentation cited as the primary causes (Vickery and Herkert 2001, Brennan and Kuvlesky 2005, With et al. 2008). The majority of habitat loss has involved conversion of native prairie to grain cultivation, but seeded grasslands of a single or small number of exotic grass species have become extensive throughout the Great Plains and may be an influential factor in declines of grassland birds (Delisle and Savidge 1997, Flanders et al. 2006). Results from studies on effects of exotic grass species on birds have been mixed. Some grassland birds, including species of conservation priority, can benefit from exotic grass fields if the fields meet specific area and structural requirements for breeding (Scott and Lima 2004, Jones and Bock 2005). In contrast, exotic grasslands can provide less suitable habitat for breeding birds if the plant community is simplified and supports fewer arthropods than native fields (Flanders et al. 2006, Hickman et al. 2006).

Old World bluestem, also known as yellow bluestem, (*Bothriochloa ischaemum*; OWB) is native to Eurasian grasslands, but cultivars have been widely established in the southern Great Plains for pasture and in fields reenrolled in the U.S. Department of Agriculture's Conservation Reserve Program (CRP). More than 1 million hectares of OWB have been planted in Oklahoma and Texas, and over 50% of the CRP land in some western Oklahoma counties has been planted to OWB (White and Dewald 1996, Ripper and VerCauteren 2007). Despite widespread use and invasive potential of OWB (Gabbard and Fowler 2007), few studies have examined its effects on grassland songbirds. Some evidence suggests that OWB provides inferior breeding habitat for several grassland bird species, including reduced food availability (McIntyre and Thompson 2003, Hickman et al. 2006), but previous studies have not included a sampling method that allows for robust comparisons of density among different species. Our objectives were to compare (1) breeding bird abundance, (2) vegetation structure and composition, and (3) arthropod biomass between OWB monocultures and native mixed-grass prairie.

METHODS

From May–July 2007 and 2008, we studied breeding grassland birds in the Prairie Tablelands ecoregion (Woods et al. 2005) of north-centr

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Oklahoma. Agricultural land uses dominated this region, with approximately 68% of the land area in cropland and 26% in native rangeland or seeded grasslands (U.S. Department of Agriculture [USDA] 2008). Most seeded grasslands in the region were monocultures of OWB (Ripper and VerCauteren 2007).

We identified 12 sites in Alfalfa, Garfield, and Grant counties for a paired study of six OWB and six native grass fields. All sites were located on private land and were interspersed to account for any local variation in soil types or precipitation. We selected study fields representative of the region, targeting level or gently rolling topography in grasslands of 60–100 ha. All fields were grazed by cattle, but landowners varied stocking rates throughout the study; grazing was therefore classified using measured vegetation characteristics and a relative estimate of cattle density. Eleven fields were lightly grazed, and one native field was heavily grazed. Four of the OWB fields were also managed for hay production, but all haying occurred during late summer after sampling had concluded (George et al. 2009).

We estimated breeding bird abundance and density at all fields using distance sampling (Buckland et al. 2001). We used aerial photos from the National Agricultural Imagery Program (www.fsa.usda.gov/FSA) to establish two 750-m long transects in each field. In locating specific sampling transects, we applied a 50-m buffer to field edges and riparian zones and avoided sampling along parallel orientations to such features to reduce bias in detection distances. We used a hand-held global positioning system (GPS) unit to record transect locations.

Each field was sampled 3–5 times in 2007 and five times in 2008 from mid-May through mid-July on days with no rain and light winds (<10 km/hr). Sampling consisted of a single observer (ADG) walking the transect line during morning hours (0530–1000 CDT) and recording all individuals of all species visually or aurally detected. The observer used a laser rangefinder to estimate the distance (m) and a magnetic compass to estimate the angle (azimuth degrees) to each individual at its initial point of detection. We excluded from analysis individuals detected flying over the field or using the edge between the field and another cover type.

Following field sampling, we used the distances and angles recorded to estimate detection functions for different species in program DISTANCE (Thomas et al. 1998, Buckland et al. 2001). Because the detection functions for different species permit a robust estimate of density, we could compare breeding density among species (Buckland et al. 2001, Diefenbach et al. 2003). Statistical analyses were restricted to those species detected on ≥25% of the surveys within a field type, in at least one year. Using DISTANCE, we estimated breeding density (number of individuals/ha) of Grasshopper Sparrows (*Ammodramus savannarum*), Eastern Meadowlarks (*Sturnella magna*), and Dickcissels (*Spiza americana*) in native and OWB fields in 2007 and 2008. To minimize error resulting from differences in detectability in analysis of less abundant species, we compared detection-distance histograms among samples and truncated data to within 25 m of transects, with the assumption that all individuals were detected within this distance (Buckland et al. 2001). We used the truncated data to estimate densities of less abundant species as the number of individuals/ha. Breeding density was estimated for each visit to a site and averaged within years for statistical analyses. We pooled data when we did not detect a year effect. We used a Wilcoxon signed-rank test for differences between years within field types and a Mann-Whitney *U*-test to detect differences between field types. All statistical comparisons were made using SPSS 16.0 (SPSS Institute Inc. 2008) with alpha = 0.05.

In 2007 and 2008, we quantified vegetation structure during the third week in July, when most individuals had concluded breeding behaviors (e.g., nesting, territorial defense, singing) for the season. Vegetation was sampled at 30 randomly selected points along the bird sampling transects (George et al. 2009). We used a Robel pole (Robel et al. 1970) to estimate vertical obstruction from the 4 cardinal directions at each point along the transect, resulting in 120 estimates/field. The standard deviation of vertical obstruction at each point (within a 4-m radius) and across each sampling transect (750 m) were used as measurements of structural heterogeneity at the point and field scales (e.g., Fuhlendorf and Engle 2004). To determine herbaceous canopy cover, we visually estimated relative amounts of OWB, other grasses, forbs, litter, and bare ground in seven cover classes (0%, >0–5%, >5–25%, >25–50%, >50–75%, >75–95%, >95–100%) in a 1-m^2 sampling frame placed 3 m from the sampling transect in the four cardinal directions at the same

FIG. 1. Mean density of bird species detected on at least 25% of surveys within a field type (Old World bluestem [OWB] monocultures and native mixed-grass prairie) during the breeding season in north-central Oklahoma in 2007 and 2008. Species included Grasshopper Sparrow (GRSP), Dickcissel DICK), Eastern Meadowlark (EAME), Brown-headed Cowbird (BHCO), Killdeer (KILL), Common Nighthawk (CONI), Mourning Dove (MODO), Northern Bobwhite (NOBO), and Lark Sparrow (LASP). Error bars represent SE; small "a" indicates differences at $P < 0.05$.

randomly-located points used for estimates of vertical obstruction ($n = 120$ points/field). Cover estimates included only plants rooted completely inside the frame. We used the midpoint of each cover class to calculate percent canopy cover (Daubenmire 1959, Towne et al. 2005). We also recorded the maximum vegetation height inside the sampling frame. Repeated-measures analysis of variance (ANOVA) was used to compare vegetation structure and composition characteristics between the two field types with year as the repeated measure. We identified relationships among vegetation variables and bird species densities using a Spearman rank correlation.

To determine effects of OWB on food availability for breeding grassland birds, we collected and compared arthropod samples in each site during the third week of July 2007 and 2008. Heavy rains in 2007 prevented us from collecting comparable samples earlier in the season. We sampled arthropods with a 32-cm diameter sweep net in 2007 and a gasoline-powered, hand-held vacuum (D-vac; Dietrick et al. 1960) in 2008 along the same transects used to sample birds and vegetation. We walked slowly along a randomly chosen 100-m section of each transect, sweeping the top of the vegetation with the D-vac or net (100 sweeps). Samples were frozen following collection. We sorted all arthropods by order and obtained dry biomass (g/transect) for each order in each field. Differences in biomass between OWB and native sites for the most abundant arthropod orders were tested using ANOVA. Because of differences in sampling methods between 2007 and 2008, we made no comparison of arthropod biomass between years.

RESULTS

We observed 40 bird species in native fields and 28 in OWB monocultures during the breeding seasons of 2007–2008. Detection rates for nine species exceeded 25% in at least one field type, permitting comparisons of breeding density for those species (Fig. 1). We detected no year effects on breeding density ($P > 0.05$) for any of these species between 2007 and 2008, so we pooled data for tests of differences between field types. Grasshopper Sparrow was the most abundant species, followed by Eastern Meadowlark and Dickcissel. These were the only species detected frequently enough to obtain an adequate sample size ($n > 60$ detections) for density estimation with DISTANCE. Density of Grasshopper Sparrows was greater in OWB monocultures than in native fields ($U = 2.0$, $P = 0.01$). Densities of Dickcissels and Eastern Meadowlarks did n

TABLE 1. Vegetation characteristics (mean and SE) of Old World bluestem monocultures (OWB) and native mixed-grass prairie in north-central Oklahoma in July 2007 and 2008.

	July–2007		July–2008	
	OWB	Native	OWB	Native
	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
Grass cover (%)	72.48 ± 3.49	52.57 ± 8.57	50.49 ± 16.06	62.05 ± 10.76
Forb cover (%)[a]	1.26 ± 0.63	14.99 ± 3.84	1.62 ± 0.66	10.60 ± 2.98
Litter cover (%)[a,b]	3.01 ± 0.73	5.76 ± 0.91	7.66 ± 2.53	19.75 ± 3.63
Bare ground (%)	27.26 ± 4.13	25.18 ± 7.40	25.15 ± 5.76	28.59 ± 10.48
Vegetation height (cm)[b]	76.93 ± 6.12	91.52 ± 18.87	47.74 ± 3.07	59.71 ± 9.90
Vertical obstruction (dm)[b]	3.96 ± 1.14	5.51 ± 1.95	1.79 ± 0.22	2.32 ± 0.57
Point heterogeneity[b]	0.60 ± 0.04	1.24 ± 0.34	0.53 ± 0.03	0.69 ± 0.15
Field heterogeneity	1.22 ± 0.16	2.36 ± 0.73	1.10 ± 0.22	1.08 ± 0.19

[a] $P < 0.05$ between field types
[b] $P < 0.05$ between years

differ between the two field types. Of the less abundant species, Killdeer (*Charadrius vociferus*; $U = 3.5$, $P = 0.01$) occurred at greater densities in fields planted to OWB, whereas Northern Bobwhites (*Colinus virginianus*; $U = 3.0$, $P < 0.01$) and Lark Sparrows (*Chondestes grammacus*; $U = 9.0$, $P = 0.05$) occurred at greater densities in native mixed-grass prairie.

We detected differences in structure and composition of vegetation variables between years and field types (Table 1). In both field types we observed less litter cover ($F_{1,10} = 10.1$, $P = 0.01$) and greater vegetation height ($F_{1,10} = 39.63$, $P < 0.001$), vertical obstruction ($F_{1,10} = 13.1$, $P = 0.01$), and point heterogeneity ($F_{1,10} = 8.56$, $P = 0.02$) in July 2007 than July 2008. Only forb cover ($F_{1,10} = 21.2$, $P = 0.002$) and litter cover ($F_{1,10} = 9.09$, $P = 0.017$) were greater in native fields than OWB in both years.

Spearman-rank correlations revealed relationships between seven of nine bird species and vegetation characteristics. Density of Dickcissels was correlated positively with forb cover ($r = 0.43$, $P = 0.05$), vertical obstruction ($r = 0.60$, $P < 0.01$), and point structural heterogeneity ($r = 0.46$, $P = 0.03$). Density of Brown-headed Cowbirds (*Molothrus ater*) was correlated negatively with vegetation height ($r = -0.43$, $P = 0.04$), and vertical obstruction ($r = -0.52$, $P = 0.01$). Density of Killdeer was correlated negatively with forb cover ($r = -0.51$, $P = 0.02$), vertical obstruction ($r = -0.44$, $P = 0.04$), and point structural heterogeneity ($r = -0.44$, $P = 0.04$). Density of Mourning Doves (*Zenaida macroura*) was correlated positively with bare ground ($r = 0.56$, $P = 0.01$). Density of Northern Bobwhites was correlated positively with forb cover ($r = 0.54$, $P = 0.01$) and litter cover ($r = 0.58$, $P < 0.01$), and negatively correlated with bare ground ($r = -0.53$, $P = 0.01$). Density of Lark Sparrows was correlated negatively with vegetation height ($r = -0.52$, $P = 0.01$).

Total arthropod biomass was higher in native fields than OWB monocultures during both years (Fig. 2): 2007 ($F_{1,10} = 4.59$, $P = 0.05$) and 2008 ($F_{1,10} = 11.83$, $P = 0.01$). Orthoptera was the dominant arthropod order by biomass in both sampling periods, followed by Hemiptera, Coleoptera, and Aranaea (Fig. 3). Biomass of Orthoptera ($F_{1,10} = 10.12$, $P = 0.01$) and Coleoptera ($F_{1,10} = 4.64$, $P = 0.05$) in July 2007 and Orthoptera ($F_{1,10} = 6.90$, $P = 0.03$), Hemiptera ($F_{1,10} = 21.17$, $P < 0.01$), and Coleoptera ($F_{1,10} = 5.14$, $P = 0.05$) in July 2008 was greater in native-mixed grass prairie than in seeded monocultures.

DISCUSSION

In our study, fields seeded to OWB and managed as monocultures supported fewer bird species than native fields. We found at least 12 more species using native fields than using OWB fields in 2007–2008. A greater biomass of arthropods, especially among the Orthoptera, serves as a potential mechanism for that difference in species richness between native and exotic grass fields. Exotic grass fields, however, did provide habitat for some species of native grassland birds. For example, Grasshopper Sparrows occurred in OWB fields at almost twice the density of native fields.

Our results suggest that grass species composition is less influential than vegetation structure

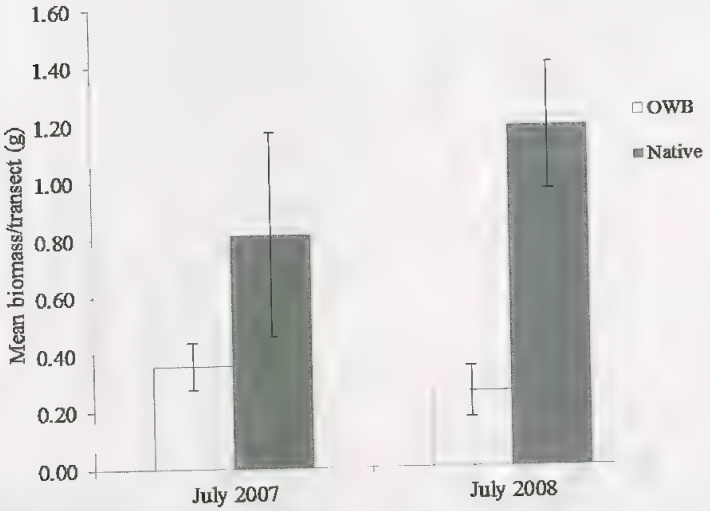

FIG. 2. Mean arthropod biomass (g) per transect in Old World bluestem monocultures (OWB) and native mixed-grass prairie in July 2007 and 2008. Error bars represent SE. Arthropod biomass was higher in native fields in both years.

in providing habitat for some species of grassland birds (Jones and Bock 2005). In eastern North America, exotic grass fields support multiple species of grassland birds (e.g., Norment 2002, Scott et al. 2002), and Jones and Bock (2005) found that Botteri's Sparrows (*Peucaea botterii*) used exotic grasses in Arizona. In some instances, however, high breeding densities have been negatively correlated with individual reproductive success (Van Horne 1983).

Other studies have shown that Grasshopper Sparrows selectively nest in larger patches of relatively homogeneous habitat with little shrub cover, less vertical cover, and relatively shorter vegetation (Vickery 1996, Delisle and Savidge 1997). Because OWB fields are often established on former cropland and are managed as monocultures, they generally meet these characteristics. Although vertical obstruction and vegetation height did not differ between OWB monocultures and native fields in our study, OWB fields did provide larger tracts of homogenous habitat, devoid of woody plants, compared to native grass fields. However, the difference in breeding density of Grasshopper Sparrows between OWB and native grass fields was unlikely a result of landscape differences between the two types of fields. All fields occurred in similar agricultural-grassland matrices and all were large (60–100 ha) relative to the minimum area requirements reported for Grasshopper Sparrows in other parts of their range where they are abundant (e.g., 10–30 ha, Herkert 1994; 8–12 ha, Helzer and Jelinski 1999).

In contrast to Grasshopper Sparrows, both Northern Bobwhites and Lark Sparrows were less abundant in the OWB than in native fields. At least 10 additional species were absent from OWB fields but encountered at more than one native field. This suggests that exotic plant invasions reduce habitat suitability for various bird species (Flanders et al. 2006, Hickman et al. 2006). In addition to vegetation structure, some birds may choose habitats on the basis of species composition of plant communities (Block and Brennan 1993, Rotenberry and Wiens 1998). Although we did not compare species-specific plant composition, we did find a greater percentage of forbs in native fields. Because OWB fields were seeded and managed as monocultures, they contained lower plant species richness and structural diversity, resulting in reduced habitat for certain grassland birds.

Densities of several bird species were related to vegetation characteristics that are influenced by management. For example, Dickcissels colonize fields with relatively tall vegetation, dense cover, a well-developed litter layer, a conspicuous forb and/or woody component, and elevated song perches (Temple 2002). These elements can be found in fields managed for a variety of uses including hayfields and pastures, and grass species composition may have minor bearing on selection if specific structural features are represented

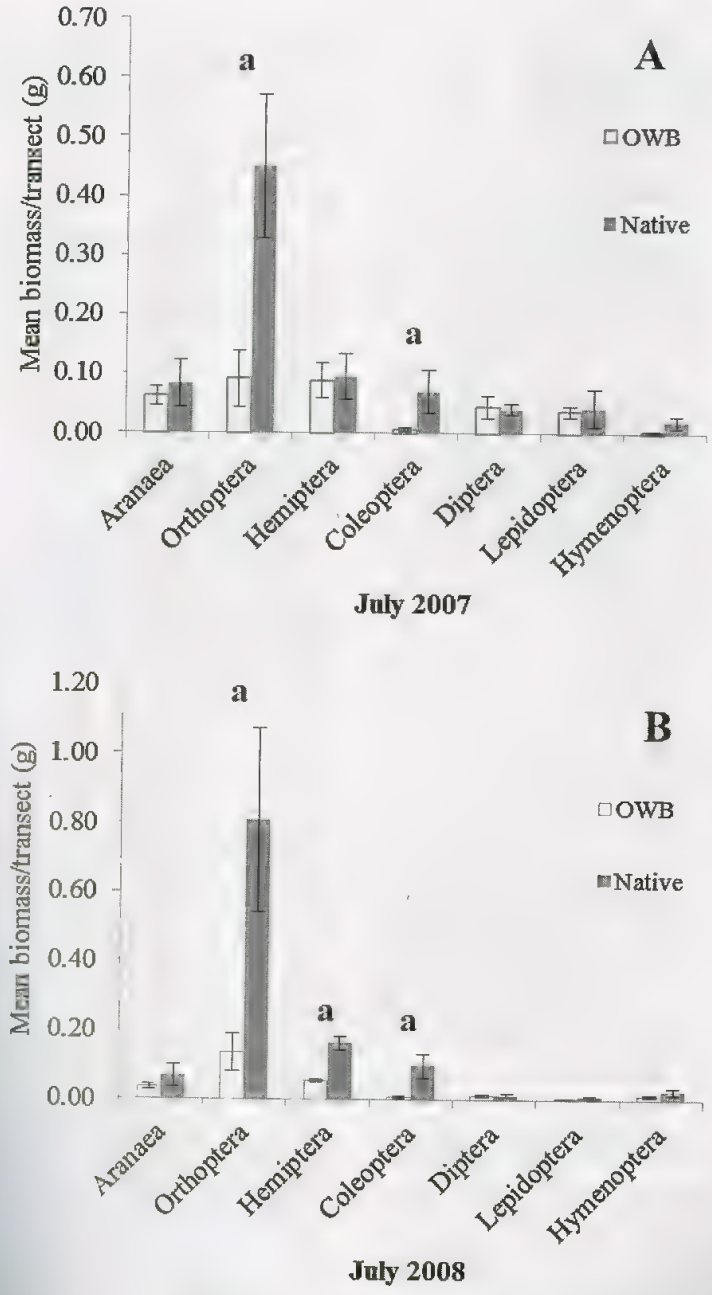

FIG 3. Mean biomass (g) per transect of dominant arthropod orders in Old World bluestem monocultures (OWB) and native mixed-grass prairie in A) July 2007 and B) 2008. Error bars represent SE, and small "a" indicates differences at $P < 0.05$.

Rahmig et al. 2008). We found the density of Dickcissels to correlate positively to estimates of forb cover, vertical obstruction, and field structural heterogeneity, regardless of field type.

Exotic grasses may not support appropriate prey for birds. The fact that arthropods are crucial to birds during the breeding season has been well established (Wiens 1973). In this study, biomasses

of taxa that are primary food sources for birds (e.g., Orthoptera, Hemiptera, and Coleoptera) were lower in OWB fields than in native fields. It is not clear why biomass of Hemiptera was higher in native grass fields in 2008 but did not differ between field types in 2007. However, in a comparison study, Doxon et al. (2011) found sweep-net samples biased against Hemiptera, which might explain the overall lower biomass of this group in both field types in 2007. The difference in total arthropod biomass was driven primarily by Orthoptera, for which biomass was more than 4× greater in native than in OWB fields. While structural variation among fields likely influenced local arthropod diversity and abundance, we found no differences in vegetation structure between field types, suggesting that OWB fields support fewer arthropods. McIntyre and Thompson (2003) and Hickman et al. (2006) likewise indicated low biomass of arthropods in OWB fields, potentially limiting populations of some bird species.

In recent years, seeding with native mixes has been recommended by natural resource agencies (e.g., Miller 2013) but seeded OWB monocultures, established in the 1980s–1990s, are still abundant throughout the southern Great Plains, and are still being established for hay production in this region. More bird species use exotic grass monocultures than use crop fields (Johnson and Schwartz 1993, Best et al. 1997), and some of those species might thrive in exotic grasses (Jones and Bock 2005). Our study and others (Flanders et al. 2006, Hickman et al. 2006, Rahmig et al. 2008), however, suggest that native grasslands are more likely to support the full complement of birds in a region. In light of the negative impacts of exotic species on native biodiversity in general (Mack et al. 2000), promotion of native grasslands in future conservation programs might enhance the integrity of grassland ecosystems.

Future research should be directed toward the potential influence of OWB on mechanisms of bird reproductive success and source-sink dynamics of common and conservation-priority species. For example, With et al. (2008) expressed concern that Dickcissels, Eastern Meadowlarks, and Grasshopper Sparrows did not have regionally viable populations in the Flint Hills ecoregion of eastern Kansas and Oklahoma. In particular, research into the reproductive success, survivorship, and site fidelity of Grasshopper Sparrows in OWB fields could improve our understanding of landscapes with a high proportion of CRP enrollments that include exotic grass monocultures. Understanding the mechanisms by which exotic grasses influence native ecosystems will allow prioritization of conservation activities and mitigation of negative impacts through more effective management practices.

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NESTLING PROVISIONING BY HAIRY AND WHITE-HEADED WOODPECKERS IN MANAGED PONDEROSA PINE FORESTS

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ABSTRACT.—Parental roles in nestling provisioning and composition of prey brought to nestlings are not well-studied for North American woodpeckers (Picidae). We studied nestling diets and the role of adult Hairy (*Picoides villosus*) and White-headed woodpeckers (*Picoides albolarvatus*) in provisioning nestlings and nest sanitation during 2009–2011 in managed ponderosa pine (*Pinus ponderosa*) forests, Cascade Range, Washington, USA. Male White-headed Woodpeckers removed fecal material from cavities more frequently than females; a difference we did not observe between sexes in Hairy Woodpeckers. Male and female White-headed Woodpeckers, and female Hairy Woodpeckers, fed significantly more small (beak closed when holding prey) than large prey (beak unable to close when holding prey) to nestlings. We did not find differences in provisioning rates by sex of the parent, by nestling age, or by date of provisioning trip for either species. Morisita's Index (C) of diet overlap showed a large similarity in the nestling diets of Hairy and White-headed woodpeckers ($C = 0.81$), and dietary niche breadth was low for both species. Of the prey we identified, larvae of wood-boring beetles (Coleoptera: Cerambycidae and Buprestidae) were most frequently fed to nestlings by both species. White-headed Woodpeckers fed caterpillars (Lepidoptera) and winged prey to nestlings more often than Hairy Woodpeckers. The diet of Hairy Woodpecker nestlings did not change appreciably over the nesting season, with wood-boring beetle larvae having the highest relative frequency for most of the breeding period. In contrast, relative frequency of wood-boring beetle larvae in the diet of White-headed Woodpecker nestlings declined toward the end of the breeding period as the relative frequency of caterpillars increased. Our results suggest that both sexes of these woodpeckers contribute equally to nestling provisioning.
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Key words: Hairy Woodpecker, nest sanitation, nestling provisioning, *Picoides*, ponderosa pine, White-headed Woodpecker, woodpecker.

Evaluating rates of nestling provisioning by adult birds provides insight into foraging strategies and reproductive effort (Barba et al. 2009). In most biparental avian species, both males and females provision the young, although this task is not always shared equally between sexes (Nordlund and Barber 2005). In woodpeckers (Picidae), biparental care is thought to be necessary to successfully raise offspring (see Wiebe 2005 for an exception in the Northern Flicker [*Colaptes auratus*]), resulting in social monogamy for most woodpecker species (Chazarreta et al. 2011). Unlike other avian groups, such as passerines, where females generally invest more than males in raising offspring (Wiktander et al. 2000), male woodpeckers contribute significantly to raising young by performing nocturnal incubation and brooding (Wiktander et al. 2000, Wiebe 2008), and contribute equally to or greater than females in regard to nest sanitation and feeding of nestlings (Hogstad and Stenberg 1997, Michalek and Winkler 2001, Rossmanith et al. 2009, Chazarreta et al. 2011).

Few studies address nestling provisioning rates and nestling diets for North American woodpeckers. For example, we found provisioning rates for only 8 of the 20 non-cooperatively breeding woodpeckers that nest north of Mexico (American Three-toed Woodpecker [*Picoides dorsalis*; Gibbon 1966], Nuttall's Woodpecker [*P. nuttallii*; Miller and Bock 1972], Yellow-bellied Sapsucker [*Sphyrapicus varius*; Kilham 1977], Pileated Woodpecker [*Dryocopus pileatus*; Bull and Meslow 1988], Gila Woodpecker [*Melanerpes uropygialis*; Martindale and Lamm 1984], Lewis's Woodpecker [*M. lewis*; Tashiro-Vierling 1994], Downy Woodpecker [*P. pubescens*; Hawkins and Ritchison 1996], and Northern Flicker [Wiebe and Elchuk 2003]). In addition to quantifying provisioning rates, identification of important arthropod prey to nestling woodpeckers will increase understanding of breeding season habitat use because woodpecker prey can be linked to specific habitat features (e.g., Cerambycid... larvae are linked to recently dead wood, ... beetles [Coleoptera] are linked to diseased ... stressed trees).

The White-headed Woodpecker (*P. albolarvatus*) is primarily associated with pine (*Pinus spp.*

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forests resulting in a narrow and fragmented distribution throughout the western United States and southern British Columbia (Garrett et al. 1996). In the Pacific Northwest, the White-headed Woodpecker primarily inhabits interior, ponderosa pine (*Pinus ponderosa*) dominated forests along the eastern slope of the Cascade Range and in the Blue Mountains. Although once labeled as one of the most poorly studied woodpeckers in North America (Garrett et al. 1996), recent studies have focused on foraging (Kozma 2010), nesting habitat (Buchanan et al. 2003; Kozma 2011, 2012), phylogeography (Alexander and Burns 2006), and reproductive success (Wightman et al. 2010, Hollenbeck et al. 2011, Kozma and Kroll 2012). Despite these studies, information on sex-specific roles in provisioning nestlings and nest sanitation, as well as detailed information on the diet of nestlings, is lacking.

The Hairy Woodpecker (*P. villosus*) occurs in a wide variety of forest types in North America (Jackson et al. 2002) and occurs throughout the range of the White-headed Woodpecker. In contrast to the White-headed Woodpecker, the reproductive biology of the Hairy Woodpecker has received greater attention. However, the diet of Hairy Woodpecker nestlings has not been studied in detail and considerable variation exists in parental care demonstrated by this species (Jackson et al. 2002). For example, Kilham (1968) found that female Hairy Woodpeckers fed nestlings up to four times more frequently than males, whereas de Kiriline Lawrence (1967) found that both sexes fed nestlings at nearly equal rates. These studies were conducted in the central or eastern United States and Canada; the results of which may differ from areas in the western portion of the species' range.

We evaluated the diets of both Hairy and White-headed woodpecker nestlings and sex-specific roles of adults when provisioning nestlings in ponderosa pine-dominated forests of the eastern Cascade Range, Washington, USA. Specifically, our objectives were to: (1) determine if differences exist between the sexes in their rate of nestling provisioning and nest sanitation, and the size of prey delivered to nestlings for both species, (2) describe to the finest taxonomic level the diversity and frequency of prey fed to nestlings, and (3) compare nestling diet overlap between the two species.

METHODS

Study Area.—We conducted this study along the eastern slope of the Cascade Range in southern Kittitas and Yakima counties, Washington (46° 46′ N, 120° 59′ W), from 2009–2011. The climate in this region is characterized by hot, dry summers, with over 80% of the annual precipitation occurring in winter, primarily as snow (Wright and Agee 2004). The eastern slope of the Cascades is characterized by complex topography (Everett et al. 2000). Our study area contained 24 sites located on lands managed by Okanogan-Wenatchee National Forest (10 sites), Washington Department of Natural Resources (10 sites), and three private landowners (four sites). Through yearly censusing of known breeding territories of White-headed Woodpeckers, we determined that each site contained only one White-headed Woodpecker breeding pair. Each site consisted of the forested stand the pair was known to occupy where the mean breeding season home range from 95% fixed kernel estimates is 105 ha (SD = 36 ha, n = 13; T. Lorenz, unpubl. data) and all sites are part of a long-term study on the reproductive biology of White-headed Woodpeckers (Kozma and Kroll 2012). We selected these sites opportunistically based on recent sightings from regional biologists and foresters, historical records of sightings of White-headed Woodpeckers (Buchanan et al. 2003), and by finding breeding pairs opportunistically in the study area as we conducted field work. We easily located nesting areas of Hairy Woodpeckers, because Hairy Woodpeckers are common in our study area and occurred in all breeding territories of White-headed Woodpeckers.

The study area contained a mix of tree species dominated by ponderosa pine, with lower abundances of Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), grand fir (*Abies grandis*), and quaking aspen (*Populus tremuloides*; Kozma 2011). Antelope bitterbrush (*Purshia tridentata*), wax currant (*Ribes cereum*), snowbrush ceanothus (*Ceanothus velutinus*), common snowberry (*Symphoricarpos albus*), and shinyleaf spiraea (*Spiraea betulifolia* var. *lucida*) were dominant understory plants. In general, ''hot-dry shrub/herb'' (ponderosa pine/bitterbrush/bluebunch wheatgrass [*Pseudoroegneria spicata*]) and ''warm-dry shrub/herb'' (Douglas-fir/bitterbrush/bluebunch wheatgrass) vegetation types dominated the study area (Harrod et al. 1999). Seventeen of 24 sites occurred in unburned stands where timber had been harvested within the past 25 years. Seven sites occurred in stands that had burned at least once in the previous 12 years

and, salvage logging occurred in five of the burned stands.

Nest Searching and Monitoring.—We searched for nests from April to early-July. We systematically searched a subset of the 24 sites each year because of time constraints and because new sites were added each year as we discovered new breeding pairs. We broadcasted playback calls and drumming of Hairy and White-headed woodpeckers at random locations as we moved through known breeding territories to locate woodpeckers (Melletti and Penteriani 2003, Nappi and Drapeau 2009). We followed either sex during the nesting season to find cavities, because both sexes of these woodpeckers take part in cavity excavation, incubation, brooding, and nestling feeding. If this failed to result in locating a cavity, we followed adult distress calls or sounds of begging chicks to reveal the cavity's location. To determine the number and age of nestlings, we viewed contents of cavities up to 11 m above ground with a Tree Top Peeper IV nest-inspection system (Kozma and Kroll 2012). We estimated nestling age from the incubation start date or hatch date if known, or from feather development of young (Kozma and Kroll 2012). We calculated the nest-initiation date (day the first egg was laid) by backdating from the day of hatching or fledging, or from the estimated age of young, assuming that incubation began on the day the last egg was laid and that one egg was laid each day during the laying period (Pechacek 2006).

Nestling Provisioning.—We used a 65ED spotting scope with a XW 10 eyepiece positioned 30–50 m from the nest cavity to record feeding observations during 2-hr time periods (Schaefer et al. 2004, Rossmanith et al. 2007). Because some previous studies have shown little evidence of diurnal variation in provisioning rates for a variety of bird species (Goodbred and Holmes 1996, Sethi and Bhatt 2007, Barba et al. 2009, Maccarone et al. 2012), we made all observations from 0800–1230 hrs (Connor et al. 1999, Schaefer et al. 2004), May to July in each year. We attempted to observe each nest once when nestlings were 1–13 days old (early) and once when nestlings were 14–25 days old (late), totaling two observation periods (4 hrs) for most nesting pairs. However, in some cases, we found nests when young were older than 13 days and some nests failed before young were 14 days old, and therefore we obtained only one observation period for those nesting pairs. We dressed in camouflage clothing and positioned ourselves near shrubs or downed wood to blend into the environment and reduce stress on the parent birds, because they can become agitated with humans near their nest cavity, especially when nestlings are greater than 10 days old (JMK, pers. obs.). Although we took steps to reduce the bias of our presence affecting woodpecker provisioning behavior, adults provisioning young probably became habituated to our presence thereby modifying their behavior patterns in order to keep the observer under surveillance (Morrison et al. 2006). We feel that this did not greatly influence the rate at which they provisioned young. We began recording feeding observations after adults had resumed normal activity and no longer gave alarm calls, which usually took from 15–30 mins. If adult woodpeckers failed to resume normal activity, we abandoned the observation attempt and returned the next day.

During each observation period, we determined the age and number of nestlings using the nest inspection system, the sex of the parent delivering prey to the cavity nest, if fecal material was removed, the size and type of prey delivered, and the time elapsed between feeding visits. We considered each trip to the nest with prey as a single visit regardless of the number of prey delivered (Pinkowski 1978). We calculated provisioning rates (number of feeding trips/nestling hour) during the early and late nestling periods for males and females of each woodpecker species (Nordlund and Barber 2005, Reed et al. 2007). When calculating provisioning rates, we used only those nests where we could determine the number of young (cavities ≤11 m in height). We were unable to view the contents of only two Hairy Woodpecker nests and this likely did not affect our results. We classified all prey items as either small, where prey is held with the beak completely closed, or large where the beak is unable to close. We further identified prey items to order or family (e.g., adult beetle [Coleoptera], ant [Formicidae]) whenever possible. We calculated the relative frequency of occurrence for each prey type, because we were unable to identify all prey items (Rossmanith et al. 2007). When calculating the contribution of each sex to nestling care, we only used nests where we verified both parents were alive during observation periods (Nour et al. 1998, Wiktander et al. 2000).

Statistical Analysis.—To determine if sexes removed fecal material from cavities equally, we

if males brought more large prey to nestlings than females, we used a Wilcoxon signed-rank test (data did not meet the assumptions of a normal distribution; Steel and Torrie 1980, Conrad and Robertson 1993). We used 95% CI to determine if each sex brought small and large prey items equally, for both Hairy and White-headed woodpeckers. We used 95% CI to compare mean provisioning rates between broods of two, three, and four nestlings, where non-overlapping CI suggested a statistically significant difference. We used mixed models (REML) to evaluate differences in parental provisioning rates for both woodpecker species (Reed et al. 2007). Our response variable was provisioning rate and we treated sex of parent, age of nestlings, and date of provisioning trip (i.e., did seasonal variation exist in provisioning rate?) as fixed effects in our models. Given that individual nests are subsamples, we treated both year and location as random effects in our model. We fit mixed models with PROC MIXED in SAS Version 9.2 (SAS Institute 2012).

We used Morisita's index (*C*; Morisita 1959), which is considered by Smith and Zaret (1982) to be the least biased estimator of diet overlap, to compare the similarity of nestling diet between the two species (Hanula et al. 2000b). To determine the degree of dietary specialization for each woodpecker species, we calculated a standardized dietary niche breadth value (B_{st}; Lewis et al. 2006) for each nest where $B_{st} = (B - 1)/(n - 1)$, and where $B = 1/\sum p_j^2$, p_j is the proportion of individuals in prey category j, and n is the number of prey categories. We used a standardized value of B because there were unequal prey categories among nests (Lewis et al. 2006). Results are presented as mean ±1 SE unless otherwise noted.

RESULTS

We recorded 641 prey deliveries to nestlings during 32 observation periods at 22 nest cavities of Hairy Woodpeckers and 728 prey deliveries to nestlings during 45 observation periods at 28 nest cavities of White-headed Woodpeckers. Male and female White-headed Woodpeckers delivered more small prey items to nestlings than large prey items, as did female Hairy Woodpeckers (Fig. 1). No difference existed in proportion of nest visits made by male Hairy Woodpeckers with large versus small prey (Fig. 1). Male White-headed Woodpeckers brought large prey and removed fecal material during a greater proportion of nestling feedings than did females (df = 23; z = 2.4, P = 0.016 and z = 2.2, P = 0.032; respectively), whereas no difference existed between male and female Hairy Woodpeckers in the proportion of nestling feeding visits containing large prey or the removal of fecal material (df = 21, z = 1.50, P = 0.13 and z = 1.56, P = 0.12; respectively; Table 1). For both species, mean provisioning rate did not differ between broods of two, three, or four nestlings, and it declined as brood size increased (Fig. 2). Provisioning rates did not differ between female and male Hairy Woodpeckers (n = 62, $F_{1,42}$ = 2.78, P = 0.100). We found no evidence of variation in Hairy Woodpecker provisioning rate by age of nestlings (n = 62, $F_{1,42}$ = 0.11, P = 0.74) or date of provisioning trip (n = 62, $F_{1,42}$ = 0.09, P = 0.76). Similarly, provisioning rates did not differ between male and female White-headed Woodpeckers (n = 83, $F_{1,59}$ = 0.01, P = 0.95). We found no evidence of variation in White-headed Woodpecker provisioning rate by age of nestlings (n = 83, $F_{1,59}$ = 0.04, P = 0.53) or date of provisioning trip (n = 83, $F_{1,59}$ = 3.36, P = 0.070).

We identified prey items to major taxonomic group during 57% of Hairy Woodpecker (n = 365 observations) and 51% of White-headed Woodpecker (n = 372 observations) prey deliveries (Table 2). From these observations, we calculated a Morisita's index of C = 0.81. The dietary niche-breadth for the Hairy Woodpecker was low (B_{st} = 0.14 ± 0.01, range = 0.10–0.20) and nearly identical to that of the White-headed Woodpecker (B_{st} = 0.15 ± 0.01, range 0.07–0.29). Larvae of wood-boring beetles (Cerambycidae and Buprestidae), adult ants and their larvae, insect larvae, and adult beetles comprised 39, 20, 15, and 14%, respectively, of prey brought to nestlings by Hairy Woodpeckers (Table 2). Wood-boring beetle larvae, caterpillars (Lepidoptera), adult ants and their larvae, and insect larvae comprised 25, 23, 18 and 6%, respectively, of prey brought to nestlings by White-headed Woodpeckers (Table 2). Excluding adult beetles, winged prey (adult antlion [Myrmeleontidae], bumblebee [Apidae], cicada [Cicadidae], crane fly [Tipulidae], adult fly [Diptera], mayfly [Ephemeroptera], moth [Lepidoptera], grasshopper [Acrididae], and all other winged insects) accounted for 12% of prey brought to White-headed Woodpecker nestlings compared to only 3% of prey brought to Hairy Woodpecker nestlings.

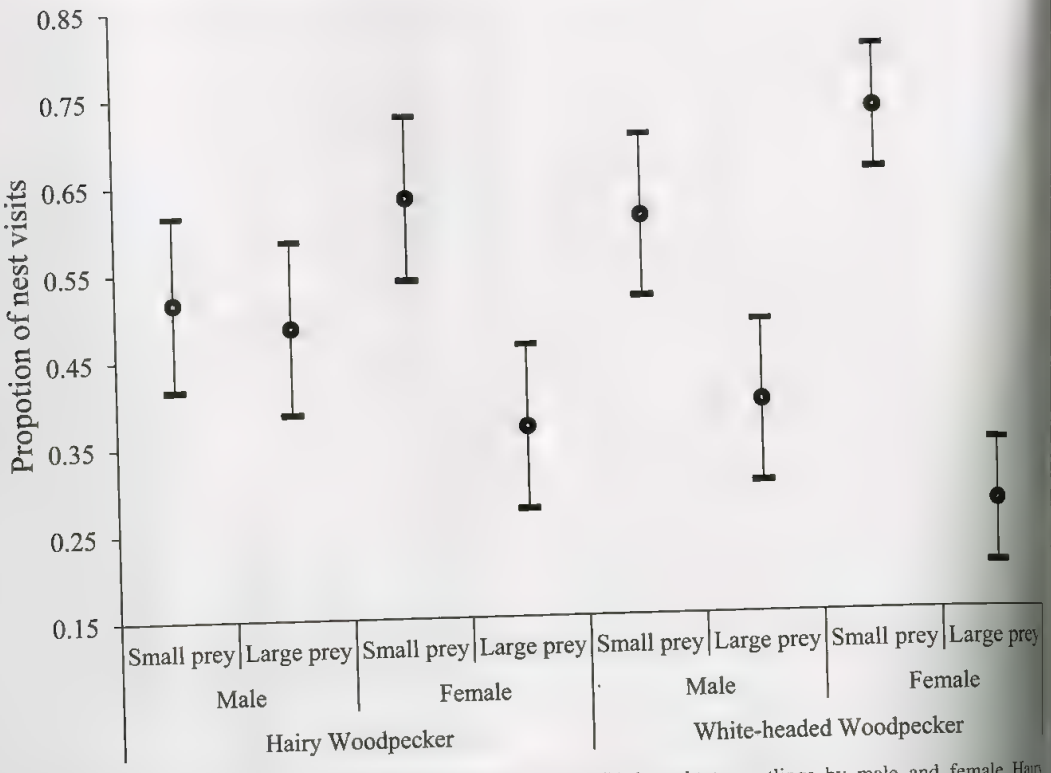


FIG. 1. Proportion of small and large prey (mean ± 95% CI) brought to nestlings by male and female Hairy Woodpeckers and White-headed Woodpeckers in managed ponderosa pine forests of the east Cascade Range Washington, 2009–2011.

The diet composition of Hairy Woodpecker nestlings did not change appreciably over the nesting season (Fig. 3). Wood-boring beetle larvae had the highest relative frequency in the nestlings' diet for most of the breeding period, with the greatest frequency occurring during the early part of the nesting season. Similarly, wood-boring beetle larvae had the highest relative frequency in the diet of White-headed Woodpecker nestlings during the first half of the breeding period, but declined steadily toward the end of the breeding period as the relative frequency of caterpillars increased nearly six-fold (Fig. 3).

TABLE 1. Nestling provisioning and nest sanitation, mean (SE), by male and female Hairy Woodpeckers (n = 2[illegible] nests) and White-headed Woodpeckers (n = 24 nests) in managed ponderosa pine forests of the eastern Cascade Range Washington, 2009–2011.

	Hairy Woodpecker		White-headed Woodpecker	
	Male	Female	Male	Female
Proportion of visits with large prey	0.49 (0.05)	0.37 (0.05)	0.39 (0.04)	0.27 (0.03)
Proportion of visits with fecal removals	0.16 (0.03)	0.12 (0.05)	0.21 (0.04)	0.08 (0.02)
Early[a] feeding rate (deliveries/nestling/hour)[b]	1.7 (0.2)	1.7 (0.3)	1.6 (0.1)	1.6 (0.1)
Late[c] feeding rate (deliveries/nestling/hour)[d]	1.4 (0.2)	2.1 (0.3)	1.6 (0.2)	1.7 (0.3)

[a] Nestling age of 1–13 days.
[b] n = 14 Hairy Woodpecker nests and n = 21 White-headed Woodpecker nests.
[c] Nestling age of 14–25 days.
[d] n = 15 Hairy Woodpecker nests and n = 17 White-headed Woodpecker nests.

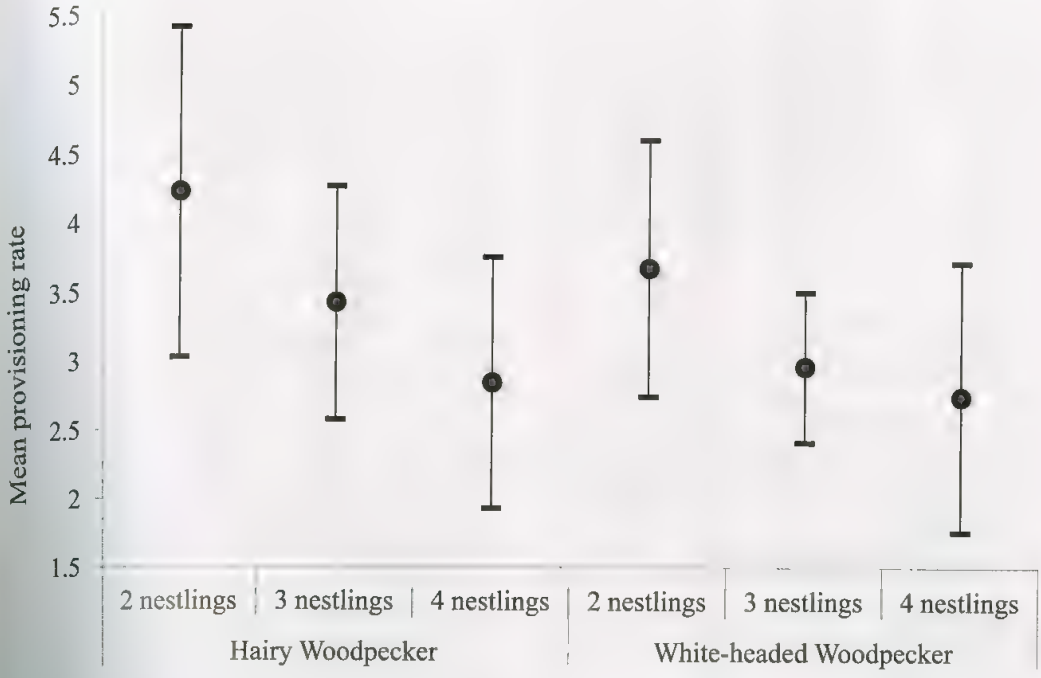


FIG. 2. Mean nestling provisioning rates (feedings/nestling/hour, 95% CI) for Hairy Woodpeckers and White-headed Woodpeckers (sexes combined) in relation to brood size in managed ponderosa pine forests of the east Cascade Range, Washington 2009–2011.

DISCUSSION

Woodpeckers are keystone species that serve critical roles in ecosystem dynamics (Virkkala 2006). Information on foraging ecology of woodpeckers can inform management guidelines and promote sustainable woodpecker populations at the landscape scale (Hanula et al. 2000b, Raley and Aubry 2006, Edworthy et al. 2011). For example, knowledge of nestling diets can guide requirements for retention/creation of habitat components that attract prey species used by woodpeckers during the breeding season. Comparing woodpecker provisioning rates and nestling diets across geographic areas can inform species- and region-specific management practices (e.g., moist coastal forests versus dry interior forests, old growth versus young stands; Hanula and Engstrom 2000, Hanula et al. 2000b).

We did not find differences between male and female provisioning rates for either Hairy or White-headed woodpeckers. Similar results have been found for Lesser Spotted (*Dendrocopos minor*; Wiktander et al. 2000), Nuttall's (Miller and Bock 1972), and Magellanic (*Campephilus magellanicus*; Chazarreta et al. 2011) woodpeckers. Although the sexes fed nestlings at similar rates in both species, provisioning rates may also be influenced by quantity of food brought by each sex (Wiebe and Elchuk 2003). However, we did not measure food quantity in this study. Furthermore, we did not evaluate the influence of time of day on provisioning rates because our observations occurred only in the morning. Temperature fluctuations associated with time of day may influence provisioning rate of White-headed Woodpeckers, especially later in the nesting period when surface-dwelling and aerial prey make up a greater proportion of the nestling diet (Miller and Bock 1972). Both Hairy and White-headed woodpeckers fed nestlings at similar rates regardless of nestling age or date, suggesting that older nestlings were not fed more frequently than younger nestlings, which contrasts with previous studies (Hogstad and Stenberg 1997, Wiktander et al. 2000). Although provisioning rates did not differ based on brood size for either species, provisioning tended to decline as brood size increased; a pattern also observed in the Northern Flicker (Gow et al. 2013). Our results suggest that both species may be unable to meet the food demands of larger brood sizes, because prey

TABLE 2. Percentage of nestling feeding visits made by adult Hairy Woodpeckers (n = 365 visits) and White-headed Woodpeckers (n = 372 visits) with each food type in managed ponderosa pine forests of the eastern Cascade Range, Washington, 2009–2011.

	Hairy Woodpecker	White headed Woodpecker
Wood-boring beetle larvae[a] (Cerambycidae and Buprestidae)	38.9	24.7
Ant larvae and/or adults (Formicidae)	20.0	18.2
Caterpillars (Lepidoptera)	2.7	23.1
Insect larvae	15.3	6.5
Beetle adult (Coleoptera)	13.7	5.4
Insects[b]	2.7	5.9
All other winged insects[c]	0.8	5.6
Moth (Lepidoptera)	1.6	3.8
Spider (Araneae)	3.3	1.1
Cricket (Gryllidae)	0.3	1.6
Cicada (Cicadidae)	0.3	1.1
Termites (Termitoidae)	0	0.8
Fly adult (Diptera)	0	0.5
Antlion adult (Myrmeleontidae)	0	0.3
Bumblebee (Apidae)	0	0.3
Crane Fly (Tipulidae)	0	0.3
Earwig (Dermaptera)	0	0.3
Grasshopper (Acrididae)	0	0.3
Mayfly (Ephemeroptera)	0	0.3
Snail (Mesogastropoda)	0.3	0

[a] All large larvae resembled wood-boring beetle larvae; however, some Siricidae larvae may have been present but were unidentifiable.
[b] Bolus of unidentified insects.
[c] Prey was noted to have wings, but further identification was not possible.

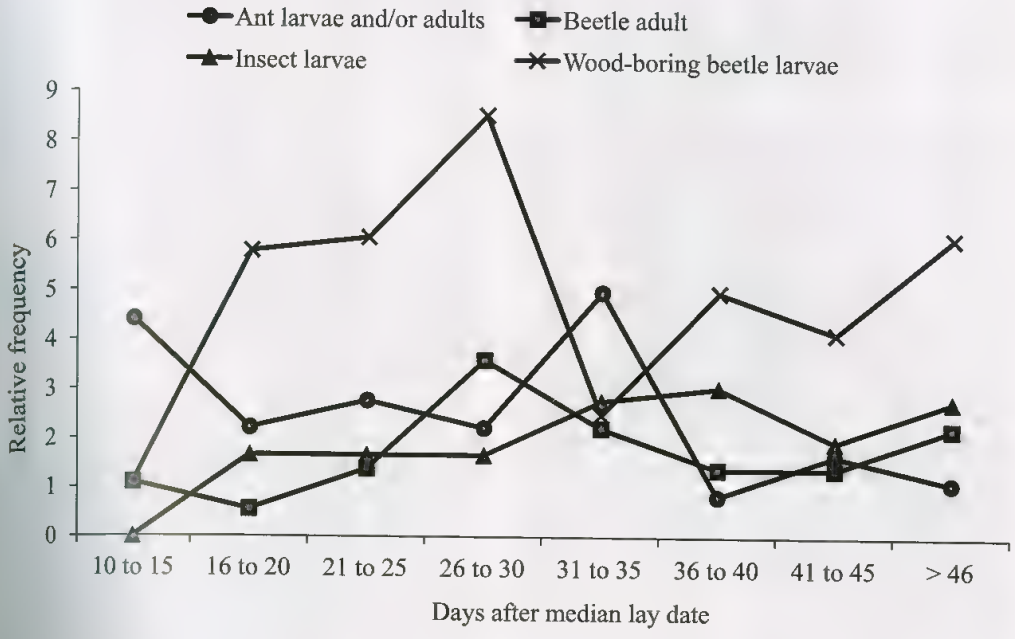
availability ultimately influences nestling provisioning rate (Smith et al. 1988, Naef-Daenzer et al. 2000) and/or adults raising larger broods may be working at their maximum capacity (Moreno 1987), especially in managed forests where foraging substrates such as snags are more limited. This conclusion is further supported by the fact that 40% of nests of White-headed Woodpeckers and 23% of nests of Hairy Woodpeckers experienced brood reduction when nestlings were <10 days old (JMK, unpubl. data). We think most brood reductions were because of causes other than predation, because many of the nestlings that died were smaller than their siblings (Stoleson and Beissinger 1997). Brood reduction occurs in other woodpeckers (LaBranche and Walters 1994, Koenig et al. 2001, Chazarreta et al. 2011) but is not well-studied.

We observed male White-headed Woodpeckers conducting the majority of nest sanitation, similar to other woodpeckers (Miller and Bock 1972, Rossmanith et al. 2009, Chazarreta et al. 2011). In addition, male White-headed Woodpeckers incubate eggs and brood the young at night, and share these duties with females during the day (Garrett et al. 1996). Male White-headed Woodpeckers may invest more effort in raising offspring than females, because females need to restore fat reserves after egg-laying. To do this, females may be consuming more large prey items rather than feeding them to nestlings, which could explain why females brought large prey to nestlings during a smaller proportion of nest visits in both species. We did not observe different fecal removal rates between male and female Hairy Woodpeckers. This differs from de Kiriline Lawrence (1967) and Kilham (1968), both of whom observed male Hairy Woodpeckers conducting most fecal removals from cavities suggesting that the role of nest sanitation is variable in this species.

The low dietary niche breadth we observed for the Hairy Woodpecker suggests prey specialization and a less diverse nestling diet (Lewis et al 2006). Larvae of wood-boring beetles, ants and their larvae, and adult beetles comprised 73% of the identifiable prey items brought to nestlings. The Hairy Woodpecker is well-known for preying on wood-boring beetle larvae (Villard and Beninger 1993, Covert-Bratland et al. 2006). Although these larvae accounted for nearly 40% of identified prey fed to nestlings, they were only present in 22% of all nest visits. Wood-boring beetle larvae, which reside in dead wood for 2–3 years, may be low in abundance in our study areas, because unburned stands have low snag densities (Kozma 2011). Few nests in burned stands were monitored within 5 years of the fire, when abundance of these larvae is thought to be highest (Murphy and Lehnhausen 1998, Covert-Bratland et al. 2006). Low snag density may explain why we observed Hairy Woodpeckers foraging for wood-boring beetle larvae in downed logs and cut stumps from previous harvests in addition to standing snags (JMK, unpubl. data). In addition to these larvae, ants and beetles are documented as important components of the diet of Hairy Woodpeckers (Koplin and Baldwin 1970, Crockett and Hansley 1978, Otvos and Stark 1985).

White-headed Woodpeckers also had a low dietary niche breadth. Wood-boring beetle larvae accounted for the highest percentage of identified prey brought to nestlings, which is surpris-

A



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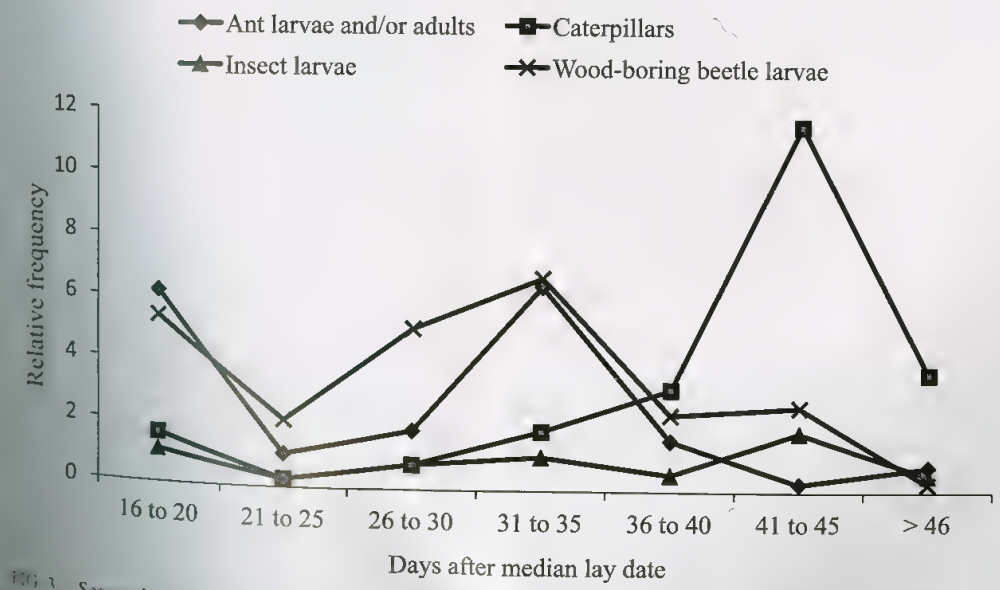

FIG. 3. Seasonal change in the four major prey types in the nestling diet of Hairy Woodpeckers (A; median laying date [illegible], n = 72 nests) and White-headed Woodpeckers (B; median laying date 28 May, n = 77 nests) in managed ponderosa [illegible] forests of the east Cascade Range, Washington, 2009–2011. Laying date refers to the date the first egg was laid.

because the White-headed Woodpecker is thought to be limited in its ability to excavate into wood while foraging. Instead, it primarily probes into bark crevices, gleans bark surfaces, and chips away bark to find prey (Koch et al. 1970, Ligon 1973, Raphael and White 1984). Similar to Hairy Woodpeckers, we only observed White-headed Woodpeckers foraging for wood-boring larvae in cut stumps (JMK and T. Lorenz, unpubl. data). Wood-boring beetle larvae are found deeper in wood during the winter (Gardiner 1957) and therefore may be more accessible to White-headed Woodpeckers during the breeding season when larvae are located closer to the bark surface. This supposition is supported by the fact that we have not observed White-headed Woodpeckers foraging for wood-boring beetle larvae from October–January (JMK and T. Lorenz, unpubl. data), although snow cover may also limit the use of stumps as a winter foraging substrate. The Three-toed Woodpecker and Pileated Woodpecker also exhibit differential seasonal use of these larvae as food (Pechacek and Kristin 2004, Raley and Aubry 2006).

In contrast to the diet of Hairy Woodpecker nestlings, caterpillars were an important component of the diet of White-headed Woodpecker nestlings later in the nestling period. Many of these were caterpillars of western spruce budworm moths (*Choristoneura occidentalis*) that adults collected from Douglas-fir needles, as well as caterpillars of the pine white butterfly (*Neophasia menapia*) taken from ponderosa pine foliage. White-headed Woodpeckers may switch to caterpillars, because they are often locally abundant (e.g., spruce budworms) and are much easier to capture than wood-boring beetle larvae (Rossmanith et al. 2007). White-headed Woodpeckers also fed more frequently on winged prey than Hairy Woodpeckers. This result was unexpected as the White-headed Woodpecker is rarely documented flycatching (Raphael and White 1984, Dixon 1995). White-headed Woodpeckers initiate nests 3 weeks later than Hairy Woodpeckers (Kozma and Kroll 2012) and may be taking advantage of caterpillars and flying insects that become more abundant and active as air temperatures increase (Markin 1982). Despite the differences we observed in the diets of nestlings of Hairy and White-headed woodpeckers, the high Morisita's index suggests that their nestling diets overlap to a considerable degree (Hanula et al. 2000b). High dietary overlap could result in interspecific competition for food, which in addition to an overlap in nest-site characteristics (Kozma 2012) and foraging behaviors (Morrison and With 1987), may account for the different nest initiation periods of these two species (Kozma and Kroll 2012). Temporal partitioning of resources is one way ecologically similar species can coexist (Hooper and Brown 1968, Toft et al. 1982) and which has been observed in other sympatric woodpeckers (Ingold 1989, Vierling et al. 2009). In addition, these woodpeckers may avoid competition by using resources in different niche dimensions (e.g., one species may forage for food in the upper canopy while the other may forage lower on the tree bole; Hayward and Garton 1988).

We note that our results may be inherently biased towards larger prey, as the smallest prey items were often unidentifiable with the methods we used. We were able to identify <60% of prey brought to nestlings, which is lower than that reported by other studies using comparable methods (Moreno 1987, Hogstad and Stenberg 1997, Rossmanith et al. 2007). We recommend that future research investigate nestling diets of these woodpeckers by using more powerful optics or automated video recorders to allow for more accurate identification of prey items and longer observational periods. We also suggest additional research investigate quality of prey delivered to nestlings, because although we observed a trend for provisioning rate to decline with larger broods, prey quality (i.e., calories) may buffer this drop if fewer, but higher quality prey are delivered. Wood-boring beetle larvae are important prey for nestlings of both woodpecker species and they are only found in recently dead trees and downed wood. Although stumps contain wood-boring beetle larvae used by woodpeckers for food, stumps from previous harvests should not be considered substitutes for snags. To improve foraging habitat during the nesting season, land managers should retain as many snags with a diameter at breast height (dbh) >35 cm and defective (e.g., burn scars, heavy mistletoe infestation, frost cracks, dead tops, etc.) live trees as possible post-harvest. Retaining or creating snags >35 cm dbh will provide greater foraging surface area leading to increased arthropod abundance and more profitable foraging (Hanula et al. 2000a, Covert-Bratland et al. 2006) while also meeting the nesting snag requirements of these woodpeckers (Kozma 2012). We

recommend that future research compare the foraging niches of both species to further investigate resource partitioning, as well as sample the availability of arthropod prey so that its influence on prey choice and the ability of adult woodpeckers to raise larger broods can be examined (Török 1990, Pechacek and Kristin 2004).

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CONTEXT-DEPENDENCE IN SEED REMOVAL BY LEKKING AND NON-LEKKING FRUGIVOROUS BIRDS IN BRAZILIAN ATLANTIC FOREST

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ABSTRACT.—Manakins are prominent fruit-eaters and seed dispersers in the Neotropics. Most manakin species establish lek areas where males devote long periods of time displaying to attract mates, interspersed with brief absences to feed on fruits located near lek areas. We compared the frequency of visits to plants, fruit handling behavior, and number of fruits ingested by the lek-forming *Manacus manacus* (White-bearded Manakin) and species of non-lekking birds in two species of fruiting trees (*Miconia rigidiuscula* and *Ocotea pulchella*) in lek and non-lek areas during the lek and non-lek periods of *M. manacus* in a threatened Atlantic forest ecosystem. During the non-lek season, *M. manacus* and non-lekking birds did not differ in the frequency of visits to *Miconia* trees near lek and non-lek areas. However, *M. manacus* swallowed a higher number of fruits near leks than non-lekking birds, while the opposite was true in non-lek areas. During the lek season, *M. manacus* visited *Ocotea* trees more frequently and swallowed more fruits than non-lekking birds in lek areas. No birds were recorded on *Ocotea* trees in non-lek areas. This study provides an example of context dependence in the quantity component of seed dispersal effectiveness in which the lek breeding system of a frugivorous species influences the identity of seed removers and the quantity of seeds removed in and around lek areas. *Received 26 November 2012. Accepted 2 February 2013.*

Key words: animal-plant interaction, Atlantic forest, courtship, fruits, *Manacus manacus*, Pipridae, seed dispersal.

Life history traits, reproductive status, and social organization of frugivorous animals may influence their movement behavior and foraging activities, thus affecting the seed dispersal service they provide (Westcott et al. 2005, Schupp et al. 2010). Lekking frugivores, for instance, concentrate their activities in and around lek areas, which may constrain the spatial extent of their fruit-eating and seed dispersal activities (Ryder et al. 2006, Karubian and Durães 2009, Cestari and Pizo in press).

Manakins are small lekking passerines that inhabit primary and secondary forests of the Neotropics (Worthington 1982, Blake and Loiselle 2002, Snow 2004). They eat a variety of small fruits (Worthington 1982, Levey 1987, Snow 2004), and may process great volumes of fruits (and seeds) in short periods of time, thus fueling their lekking activities (Höglund and Alatalo 1995, Snow 2004). During the lek season, which may last more than 6 months a year, males congregate in lek areas and perform displays for visiting females (Höglund and Alatalo 1995, Snow 2004). In the rest of the year, manakins increase their range because of the lack of commitment to reproductive activities. Thereby, the movement patterns of lekking manakins may vary according to their lek breeding phenology, with consequences for seed dispersal (Théry 1992, Krijger et al. 1997, Cestari and Pizo in press).

In this study, we tested the hypothesis that foraging activity on fruiting plants by *Manacus manacus* (Linnaeus 1766), a small lekking passerine widely distributed in the lowlands of Neotropical forests (Snow 2004), will differ from that of non-lekking frugivorous birds according to the proximity to lek areas. Manakins may be more active foragers near lek areas than non-lekking birds, particularly in relation to the frequency of visits to fruiting plants and number of fruits consumed. Manakins may thus contribute importantly to the quantitative component of the seed disperser effectiveness framework near lek areas (Schupp et al. 2010). Far from lek areas, we hypothesize that manakins visit fruiting plants at similar or less frequent rates than non-lekking birds owing to concentration of their foraging activities near lek areas.

METHODS

Study Area.—The study was conducted in the lowland forests of Itanhaém (24° 10′ S, 46° 55′ W), Peruíbe (24° 15′ S, 46° 55′ W), and Juréia Ecological Station (Iguape, 24° 28′ S, 47° 07′ W), in the state of São Paulo, southeastern Brazil. Climate is subtropical and humid. Mean an-

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rainfall is 2,278 mm with the rainy season occurring from October to April, and the dry season from May to September. Mean annual temperature is 21.4 °C, with maximum and minimum temperatures averaging 25.8 °C and 19.0 °C, respectively (Tarifa 2004). Study areas are still covered in great part with *restinga*, an Atlantic forest ecosystem threatened by urban expansion. *Restinga* is a structurally simple vegetation of halophytic herbs and shrubs close to the sea, and more complex vegetation in lowland and lower mountain forests as one moves inland (Sampaio 2005). In *restinga*, zoochorous plants usually have sharply peaked fruiting seasons, high annual fecundity, small seeds, and low rate of fruit removal (Argel-de-Oliveira 1999, Scherer et al. 2007). The most speciose plant families are Myrtaceae, Leguminosae, Rubiaceae, Melastomataceae, Lauraceae, and Annonaceae (Mamede et al. 2004). The bird community of the region includes 314 species with 76 frugivorous species (24%) (Develey 2004; CC, pers. obs.).

Bird Species.—*Manacus manacus* is a small (15–18 g) lekking passerine from lowland Neotropical forests. It has a widespread geographic distribution from Colombia to northeastern Argentina, inhabiting continuous and fragmented forests of the Amazon basin and the Atlantic forest of South America (Sick 1997, Snow 2004). In *restinga*, *M. manacus* is one of the most common understory frugivores. Secondary forests with high abundance of fruits and small upright saplings are the preferred habitat of *M. manacus* (Snow 1962). Resident males concentrate their territories in a lek area of 18–23 m × 4–9 m (Darnton 1958, Snow 1962). Lek areas may contain 2–70 main display courts, and neighboring males communicate visually and aurally. During the July to April lek season, a male spends up to 82% of its day in its lek area, making brief excursions to forage at nearby fruit sources (Cestari and Pizo 2012). Resident males are long-lived and are known to display at courts for up to 14 years (Snow 1962, Lill 1974). Females visit several resident males during the breeding season before selecting a mate for copulation. Juvenile males also practice display maneuvers in the courts mainly in periods of the day with reduced lek activity by resident males (Snow 1962).

Focal Plant Species.—Based on the availability of fruiting trees and their distances from lek areas, we chose two plant species to conduct focal observations of frugivory by *M. manacus* and non-lekking birds. *Miconia rigidiuscula* Cogn. (Melastomataceae) is a 1–15 m tall tree commonly found in the border of non-flooded patches of *restinga* forests (Martins et al. 1996). It bears small berries (3.20 ± 0.37 mm length, 3.54 ± 0.29 mm width) with 1–4 seeds per fruit ($n = 15$). Seed size is 1.21 ± 0.37 mm length, and 1.34 ± 0.22 mm width ($n = 15$). Fruits are produced from April to August, thus encompassing the end of the lek season and all the non-lek season of *M. manacus* in the region (May–Jun; CC and MAP, pers. obs.). *Ocotea pulchella* (Ness) Mez (Lauraceae) is a 4–30 m tall tree occurring in non-flooded patches of *restinga*. Its drupes have 9.49 ± 0.47 mm length and 5.37 ± 0.28 mm width ($n = 15$). Seed size is 8.19 ± 0.66 mm length and 3.87 ± 0.24 mm width ($n = 15$). The fruiting period of this species (Jul–Jan) overlapped with the lek season of *M. manacus*.

Data Collection.—To contrast the frugivory by *M. manacus* and non-lekking birds in lek and non-lek areas, we made focal observations on *M. rigidiuscula* and *O. pulchella* individuals and recorded the following parameters related to seed dispersal effectiveness (*sensu* Schupp 1993): (1) frequency of feeding visits to plants (i.e., visits with evidence of fruit consumption), (2) fruit handling behavior (fruit swallowed whole or mandibulated), and (3) number of ingested fruits. The proportion of fruits ingested by a group of birds (either *M. manacus* or all other bird species) in relation to the total number of fruits ingested was taken as its dispersal service (Schupp et al. 2010). For instance, if *M. manacus* and non-lekking birds ingested 70 and 30 fruits, their dispersal service will be 0.7 and 0.3, respectively. Lekking males of *M. manacus* feeding on fruits were identified by their straight-line flights from lek areas to focal trees. In addition, some lekking individuals were color-banded which facilitated their identifications. Bird nomenclature followed the American Ornithologists' Union (Remsen et al. 2012).

Fruiting plants were observed throughout the day (0600–1800, EST+02) from concealed places located at least 10 m from focal plants. Trees of similar height (*M. rigidiuscula*: 2.5–3.5 m, *O. pulchella*: 4–5 m), each with a full crop of ripe fruits, were chosen for observation to minimize intrinsic differences that might confound a bird's choices. Each plant species was observed for 70 hrs. The observation effort was divided equally

among plants located within 5–10 m from each of four lek areas (35 hrs) and plants located in non-lek areas (35 hrs), at least 50 m far from any lek. We observed seven fruiting individuals of *M. rigidiuscula* during the non-lek period (May–Jun 2011), three in lek areas and four in non-lek areas in Iguape. Eleven fruiting individuals of *O. pulchella*, four near lek areas and seven in non-lek areas, were observed during the lek period (Aug–Sept 2011) in Itanhaém and Peruíbe. In lek areas, the number of plants observed was limited by the availability of fruiting individuals.

Data Analyses.—Overall, few trees were visited by birds in lek (two trees of each of the focal plant species) and non-lek areas (one *Miconia*, and no *Ocotea*), which prevented us from comparing number of ingested fruit statistically. The frequency of feeding visits by *M. manacus* and non-lekking frugivorous birds to *M. rigidiuscula* and *O. pulchella* trees were compared between lek and non-lek areas using Chi-square tests (with Yates correction) or Fisher test (for small frequencies) applied to 2 × 2 contingency tables. The null hypothesis predicted equal frequencies of visits by *M. manacus* and other frugivores to trees at lek and non-lek areas. We employed the Bioestat software 5.0 for all analyses. Significance was accepted at $P \leq 0.05$.

RESULTS

Four species of birds visited *Miconia* trees: *M. manacus* and the non-lekking Flame-crested Tanager (*Tachyphonus cristatus*), Blue Dacnis (*Dacnis cayana*), and Violaceous Euphonia (*Euphonia violacea*). *M. manacus* and *T. cristatus* swallowed fruits whole, while *D. cayana* and *E. violacea* mandibulated fruits discarding part of their husks. The last two species were also considered potential dispersers of *Miconia* seeds because they swallowed the majority of the tiny seeds. *M. manacus* and the non-lekking birds did not differ in the frequency of visits to *Miconia* trees between lek and non-lek areas (Fisher test; $P = 0.16$; Fig. 1A), but the number of fruits they ingested differed: *M. manacus* ingested more fruits (27 fruits) than the other species (two fruits) near lek areas, while the opposite was true in non-lek areas (*M. manacus* ingested 11 fruits; other species ingested 20 fruits). Therefore, the dispersal service provided by *M. manacus* to *Miconia* trees near lek areas was greater than other frugivores, whereas at non-lek areas other frugivores contributed more than *M. manacus* to the dispersal of *Miconia* seeds (Fig. 1B). Together, juveniles and females of *M. manacus* ingested 27 fruits in lek areas. At non-lek areas, juveniles and females (two visits; three fruits), and adult males (four visits; eight fruits) of *M. manacus* ingested fruits.

Three species of birds visited *Ocotea* trees: *M. manacus* and the non-lekking Brazilian Tanager (*Ramphocelus bresilius*) and Rufous-bellied Thrush (*Turdus rufiventris*). They visited *Ocotea* trees near lek areas but no visits were recorded in non-lek areas. Compared with other species, *M. manacus* had greater frequency of visits near lek areas ($\chi^2_1 = 17.52$; $P < 0.001$; Fig. 1A). All the species swallowed fruits whole, but *R. bresilius* also mandibulated the fruits and discarded 40% of all the seeds consumed by non-lekking birds ($n = 15$). This seed handling behavior negatively affected the potential to disperse seeds by non-lekking birds when compared to seed treatment provided by *M. manacus*, which swallowed all fruits whole ($n = 88$). Thus, the dispersal service provided by *M. manacus* to *Ocotea* trees was also greater than other birds near lek areas (Fig. 1B). Juveniles and females (18 visits, 38 ingested fruits) as well as adult manakins (21 visits, 50 ingested fruits) consumed fruits of *O. pulchella*. They presented a clear division in the time of visits: juveniles and females visited fruiting trees before the peak period of lek activity from 0630 to 0800 hrs, and afterwards adult males predominated at fruiting plants.

DISCUSSION

Manakins evolved behavioral, morphological and physiological adaptations that allow a high rate of fruit ingestion to maintain their high metabolic rate (see Barske et al. 2011) needed to cope with the energetic costs of lekking activities (Snow 1962, Worthington 1989). Furthermore, leks of manakins usually are placed in areas with greater biomass of fruits, where females are more likely to be encountered (Emlen and Oring 19[illegible] Ryder et al. 2006). By consuming fruits near lek areas, manakins may save energy and increase their reproductive success, because they do not have to fly long distances to feed and abandon their territories and courts for long periods. During the lek period, adult males, juveniles and females stagger visitation to fruiting plants of *O. pulchella* temporally. Females and juveniles visit fruiting trees before 0800, and adult males visit trees near lek areas more frequently after 0800, when lek activities decrease. This pattern of visitation results in a prominent role of man[illegible]

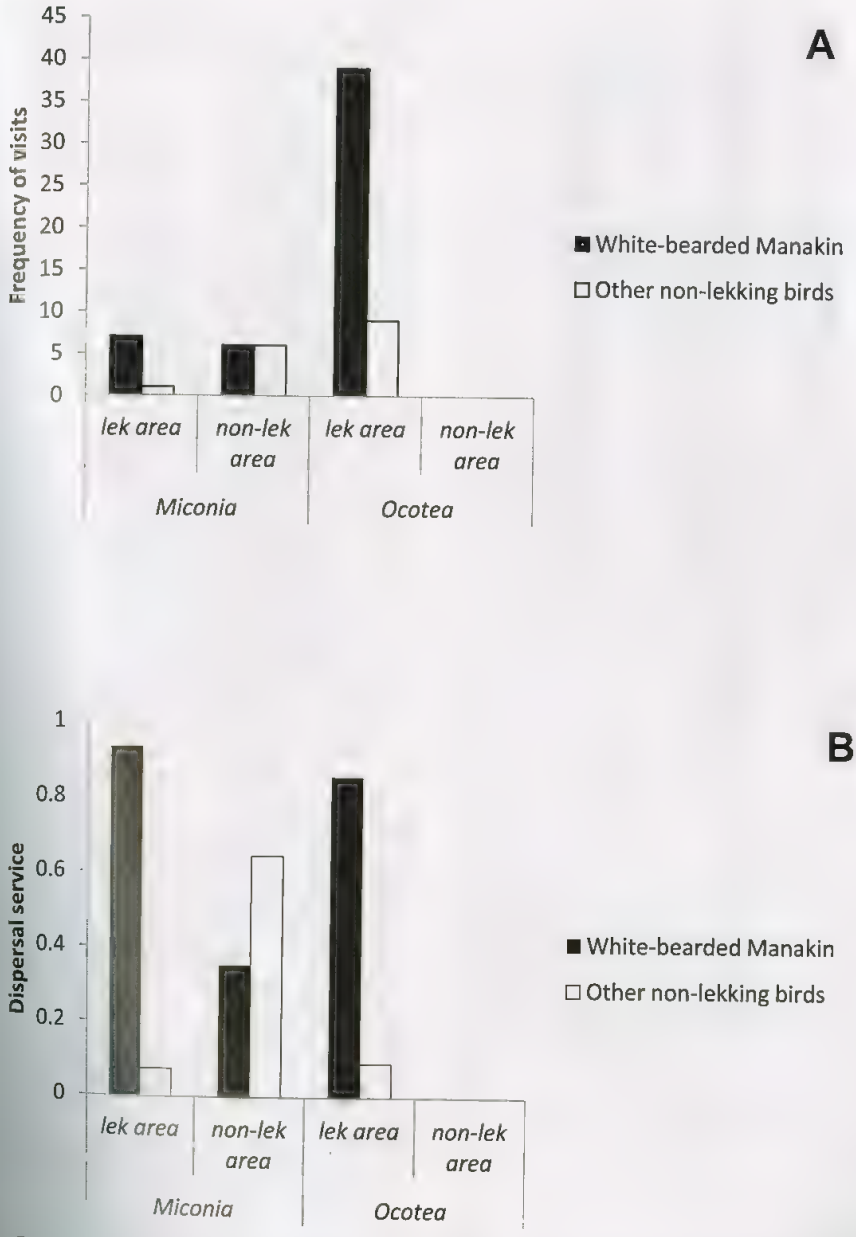

FIG. 1. Frequency of visits to *Miconia rigidiuscula* and *Ocotea pulchella* fruiting trees (A) and dispersal services (proportion of removed seeds in relation to the total number of fruits removed) (B) by White-bearded Manakin, *Manacus manacus*, and other non-lekking birds near lek areas and in non-lek areas.

n fruit consumption near lek areas. During the n-lekking period, *M. manacus* also removed re fruits of *M. rigidiuscula* in lek areas than n-lekking species. Even in the non-lekking od, manakins (mainly juveniles and females) tinue using the lek area as part of their home e, and juveniles practice display maneuvers at the lek area (Snow 1962, Ryder et al. 2006, Cestari and Pizo 2012). As a result, lek areas are not completely deserted of manakins in the non-lekking period.

The wide gape in relation to body size associated with their "gulper" strategy (*sensu* Levey 1987) also allows manakins to swallow

fruits whole that cannot be swallowed by larger birds such as some tanagers (Snow 1962). For instance, *M. manacus* had no difficulty swallowing fruits of *O. pulchella*, while the tanager *R. bresilius* employed two fruit handling techniques, swallowing the smaller fruits of *O. pulchella* whole, while mandibulating and dropping the seeds of larger fruits below mother-plants, thus wasting some fruits from the plant's perspective (Janzen 1970, Connell 1971, Schupp et al. 2010).

This study provides an example of context dependence in the quantity component of seed dispersal effectiveness mediated by the location of fruiting plants in relation to lek areas. In our system, the lek breeding system of a frugivorous bird species influences the identity of seed removers and the quantity of seeds removed in and around lek areas. We are aware, however, that information on the quality of seed deposition is needed to complete the understanding of seed dispersal effectiveness promoted by *M. manacus* and other non-lekking birds. Birds that feed on large amounts of fruit do not necessarily deposit seeds in sites viable to plant recruitment (Jordano and Herrera 1995, Loiselle and Blake 1999, Schupp et al. 2010). Seeds ingested by lekking males of *M. manacus* may be dispersed to spatially restricted areas near leks or, in a smaller scale, seeds may have a contagious dispersal (*sensu* Schupp et al. 2002, Kwit et al. 2007) to display courts. Studies in the Neotropics indicate that males of other lekking species (e.g., manakins and cotingids) clump seeds below their display perches and may influence the spatial structure and dynamics of plant populations (Théry and Larpin 1993, Krijger et al. 1997, Wenny and Levey 1998, Cestari and Pizo in press). Future studies should be directed to evaluate the fate of deposited seeds by *M. manacus*.

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USE AND CHARACTERISTICS OF TWO SINGING MODES IN PINE WARBLERS

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ABSTRACT.—North American wood-warblers (Parulidae) are well known for exhibiting two distinct singing modes: first category song, in which a single song type is sung repeatedly, usually before dawn, and second category song, in which several song types are sung in irregular sequence. Studies suggest that first category song types have higher performance characteristics and that second category song types are shared preferentially among territorial neighbors. Here we present the first formal description of two-category singing in the Pine Warbler (*Setophaga pinus*). Similar to other species in the genus *Setophaga*, Pine Warblers produce second category song before dawn and first category song primarily during daylight hours. First category songs also had significantly higher trill rates, suggesting that they are more challenging to perform. Unlike many congeners, however, Pine Warblers regularly alternate between first and second category singing throughout the day, and first category song types often appear intermixed in second category singing, including singing before dawn. Furthermore, comparisons among territorial males showed that individuals do not share song types more with neighbors than with non-neighbors. Our results suggest that Pine Warblers have two song categories similar to other *Setophaga* warblers, but singing patterns in this species differ from congeners in interesting ways that warrant further investigation. *Received 9 January 2013. Accepted 7 April 2013.*

Key words: communication, *Dendroica*, *Setophaga*, singing modes, song type sharing, vocal performance, wood-warbler

Many songbirds produce more than one song type, each of which appears to serve dual functions in both mate attraction and interactions with rival males (Collins 2004, Catchpole and Slater 2008). Several groups of songbirds, however, are known to exhibit two distinct modes, or categories, of singing, which differ in their patterns of song presentation and in the contexts in which they are performed (Spector 1992, Kroodsma 1999, Molles and Vehrencamp 1999). For example, in North American wood-warblers (Parulidae) of the genus *Setophaga* (including all former *Dendroica* and *Parula* taxa as well as *Wilsonia citrina*; Chesser et al. 2011), males produce one or a few of their song types in a highly repetitive fashion while long-distance broadcast singing during the day (first category song) and produce other song types with greater variety and at higher rates at dawn and during close-range interactions between territorial males (second category song) (Lemon et al. 1985; Kroodsma et al. 1989; Staicer 1989, 1996; Spector 1991, 1992; Wiley et al. 1994; Byers 1995; Bolsinger 2000). Species in this genus are closely related within a well-defined clade (Lovette et al. 2010, Chesser et al. 2011), based on molecular evidence. However, whether or not all members of this clade exhibit such distinct singing categories is not known (Spector 1992).

Studies have shown that first category and second category songs differ in ways other than just context and mode of presentation. Beebee (2004b), for instance, provided evidence for consistent structural differences between the first and second category songs of Yellow Warblers (*Setophaga petechia*). First category songs have significantly higher performance characteristics, measured as higher trill rates and wider frequency bandwidths, than do second category songs, suggesting that first category song types are more difficult for males to perform and thus might advertise a singer's abilities (Podos 1997, Ballentine et al. 2004). Wood-warbler song categories may differ in other ways as well, such as in note amplitudes and complexity (e.g., Spector 1992, Staicer 1996, Bolsinger 2000). Interestingly, however, the song types used in each category are usually not standardized across males within a species, with the first category song of one male often clearly resembling the second category song of another (Lemon et al. 1985; Staicer 1996, Spector 1991, 1992; Beebee 2004b).

In at least some wood-warbler species, males share significantly more of their second category song types with territorial neighbors than with non-neighbors, whereas first category songs exhibit no such patterns (e.g., Chestnut-sided Warblers, *Setophaga pensylvanica*: Byers 1995; Yellow Warblers: Beebee 2002). Such song shar-

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sharing could be adaptive if second category songs are used preferentially during territorial interactions between rival males (Spector 1992, Wiley et al. 1994, Byers 1995). Sharing song types with neighbors is known to provide important advantages for communication in some songbirds (reviewed by Catchpole and Slater 2008); however, in wood-warblers there is little evidence that males use their shared and unshared song types differently during territorial interactions (Lemon et al. 1985, Byers 1996). Moreover, playback experiments with Yellow Warblers show that males use both song categories when interacting with both males and females, suggesting that singing modes do not have distinct sex-specific functions (Beebee 2004a). Clearly, more work is needed to understand the evolution of wood-warbler song categories and the functions of these different singing modes in communication.

Here we present a quantitative analysis of song characteristics and singing behavior in the Pine Warbler (*Setophaga pinus*). Individual males in this species are known to produce more than one song type (Spector 1992, Rodewald et al. 1999). Yet, whether this species has a two-category song system typical of other *Setophaga* warblers has not been previously investigated. Previous authors have observed Pine Warblers producing two song types in alternation during daytime, suggesting that singing behaviors in this species differ from those of most congeners (Spector 1992). Males also appear to be unusual among wood-warblers in producing "double" songs, in which one song type is immediately followed by another with slightly different acoustic features (Rodewald et al. 1999). Pine Warblers are also among the few North American passerines that sing during all months of the year, including during migration (Rodewald et al. 1999). To allow comparison between this species and previously studied wood-warblers, we conducted detailed acoustic analyses of song type usage, vocal performance characteristics, and patterns of song type sharing among territorial males.

METHODS

Song Recording.—We recorded the singing behaviors of 12 male Pine Warblers from 28 June to 30 July 2011. Ten males occupied territories approximately a hectare in size at the University of Michigan Biological Station (UMBS: 45° 33′ N, 84° 42′ W), along the southern shore of Douglas Lake in Cheboygan County, Michigan, and two males had territories at the Chase Osborn Preserve (COP: 46° 21′ N, 84° 8′ W) near Duck Lake on Sugar Island, approximately 100 km to the north along the border of Michigan's upper peninsula and Ontario, Canada (Fig. 1). All territories were in mixed pine-deciduous forest dominated by red pine *Pinus resinosa* and eastern white pine *Pinus strobus*. The breeding status of each male during the sampling period was unknown. We did not color band birds for individual identification; however, only one bird was ever observed singing in each territory and neighboring birds were usually easily distinguishable by their distinct song types (see below). Thus, we are confident that identification of individuals by location was reliable. No females were ever observed singing. We recorded songs during the half hour period before sunrise and throughout the day until 1800 hrs EST. All individuals were recorded over multiple days, and we made an effort to record each individual at different times each day. All digital recordings were made at a sampling rate of 48 kHz and 16 bit depth using a Marantz solid state digital recorder (model PMD670) connected to a Sennheiser directional microphone (model ME67 with K6 power supply). We marked singing locations using a Garmin GPS 60 (Garmin Ltd., Olathe, Kansas, USA). On average, we recorded 112.1 (SE = 22.7) songs per bird (range = 24–282 songs/bird, n = 1,345 songs total) (Table 1).

Song Analysis.—The song of the Pine Warbler consists typically of a rapid, evenly spaced series of nearly identical notes (i.e., a trill), each of which is about 1–2 secs in duration (Fig. 2). We generated sound spectrograms of all recorded songs using Raven Pro 1.4 (Cornell Laboratory of Ornithology, Ithaca, New York, USA; frequency resolution = 135 Hz, time resolution = 10.7 msecs). We then sorted the songs of each male into song types based on note shape and five acoustic measurements: trill rate (notes/sec), mean note duration (msec), lowest frequency, highest frequency, and frequency bandwidth (kHz). Our methods for measuring frequency bandwidths of trills were similar to those used by Podos (1997), in which we used a power spectrum to calculate the difference between the lowest and highest frequencies with amplitudes above −24 dB relative to the peak amplitude. This amplitude threshold excluded most background noise while including most of the frequency characteristics of the bird's song (Cramer and Price 2007). For each

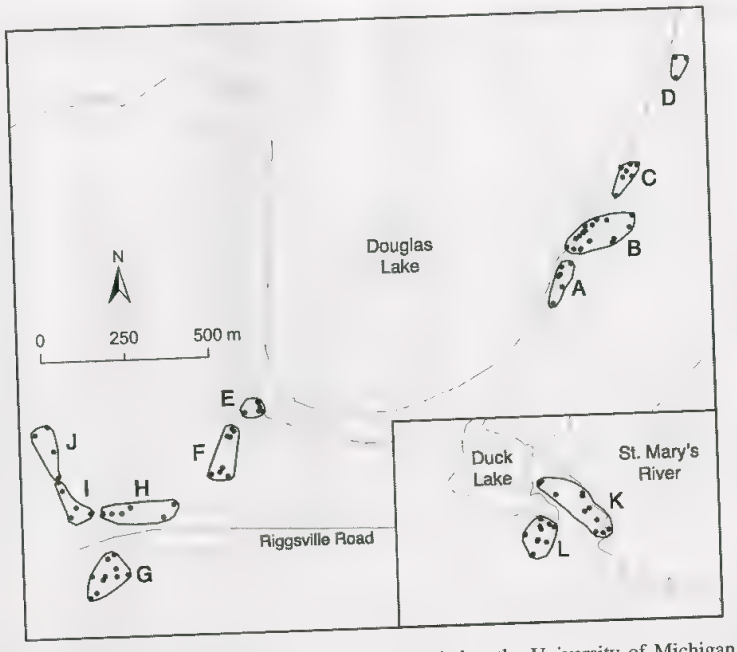

FIG. 1. Singing locations (dots) of Pine Warblers (A–L) recorded at the University of Michigan Biological Station (UMBS) and at the Chase Osborn Preserve (COP, shown in inset). Recording locations were measured using a Garmin GPS 60. Map and scale were produced using ArcGIS 9.3 (ESRI, Redlands, California).

individual bird, we considered songs with identical note shapes and similar acoustic measurements to be the same song type. We later confirmed these initial categorizations using principal components analysis (PCA; James and McCulloch 1990), as described below.

We measured singing modes (scored as "repeat mode" or "mixed mode" following Wiley et al. 1994) and singing rates (songs/min) from a subset of recordings that included bouts of 10 or more songs (n = 1,221 songs in 104 bouts). A song type was scored as occurring in repeat mode if it was repeated at least 10 times in succession, whereas songs were scored as occurring in mixed mode if more than one song type appeared in a 10 song series. Typical examples of mixed mode singing included frequently alternating song types, with each song type rarely repeated more than two or three times in succession. Following Spector (1992), we classified song types that were normally presented in repeat mode as first category songs and song types that were presented in alternation with other song types as second category songs. One bird did not provide any recordings longer than 9 songs and so could not be scored (n = 24 songs total). Average singing rates were calculated for the period before sunrise which varied during the course of the study from 0552 to 0620 hrs, and then for roughly 2-hr increments during the morning and 3-hr increments during the afternoon when activity levels were generally lower.

Vocal Performance.—To examine the relative vocal performance levels of song types, we

TABLE 1. Number of song types identified, total number of double songs recorded, and total number of songs recorded from each bird in our study.

	Individual male											
	A	B	C	D	E	F	G	H	I	J	K	L
Identified song types	4	5	3	3	1	5	4	3	3	1	1	2
Double songs	11	39	0	0	0	0	0	16	0	0	0	0
Total songs sampled	189	282	136	24	66	169	116	157	36	25	50	50

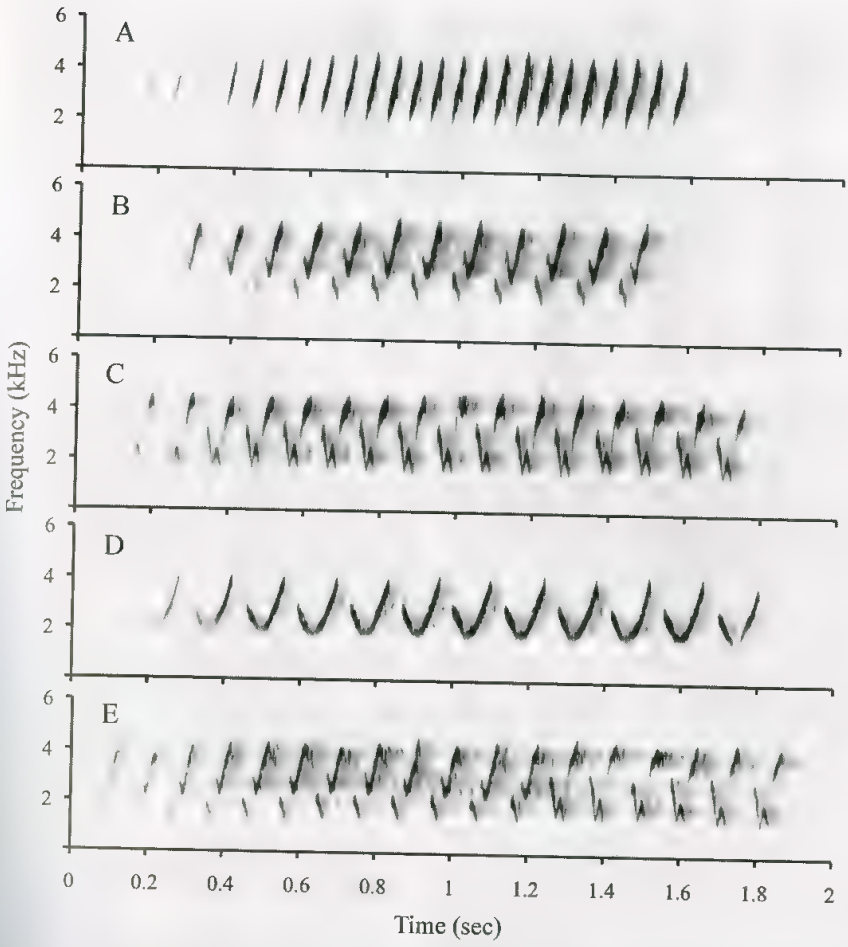

FIG. 2. A typical song type repertoire of one male Pine Warbler (n = 189 songs recorded). Four song types are shown (A-D), as well as an example of "double" song (E) in which the trills of two song types (in this case B and C) are concatenated. Song A was scored as this male's first category song type.

plotted their frequency bandwidths against trill rates. Following Podos (1997), we calculated a performance limit for our population by sorting our trill rate measurements into seven bins, each with 3 notes/sec, and then selecting the song type with the broadest frequency bandwidth in each bin for linear regression. Our bin size of 3 notes/sec maximized the number of song types included in the regression while minimizing the inclusion of lower performance songs (also see Cramer and Price 2007). Given that the upper-bound regression was significant (see Results), we then determined the relative performance level of each song type by measuring the orthogonal distance between each song type's measurements and this upper-bound regression line (Ballentine et al. 2004, Beebee 2004b, Cramer and Price 2007). Songs close to the performance limit were considered high performance songs, whereas songs farther from the performance limit were considered lower performance songs. We used these orthogonal deviation measurements to compare the mean vocal performance characteristics of first category and second category song types using an independent samples t-test. Not all of these song type measurements were statistically independent, because most males produced multiple song types. Thus, to control for potential variation among males, we further used a paired-samples t-test to compare the vocal performance characteristics of each male's first category song to the mean characteristics of his second category song types

TABLE 2. Mean (± SE) song characteristics of Pine Warblers recorded at the University of Michigan Biological Station (UMBS) and at Chase Osborn Preserve (COP). Measurements from the two locations did not differ.

	Both populations	UMBS	COP	*t* tests
	$n = 168$	$n = 143$	$n = 25$	
Measurement	Mean ± SE	Mean ± SE	Mean ± SE	*P*
Trill rate (notes/sec)	14.87 ± 0.51	15.11 ± 0.59	13.49 ± 0.81	0.113
Note length (msec)	56.7 ± 3.2	57.1 ± 3.7	54.7 ± 4.5	0.792
Low freq. (kHz)	2.99 ± 0.02	2.99 ± 0.03	2.97 ± 0.05	0.718
High freq. (kHz)	5.33 ± 0.03	5.30 ± 0.03	5.44 ± 0.09	0.106
Freq. bandwidth (kHz)	2.34 ± 0.03	2.31 ± 0.04	2.47 ± 0.09	0.105

(Beebee 2004b). All comparisons were two-tailed, and all statistical analyses were conducted using SPSS (version 18; IBM, Armonk, New York).

Song Type Sharing.—To assess song type sharing between individuals, we took measurements from five clear examples of each song type and compared these among all recorded males. Some song types exhibited obviously unique acoustic characteristics, based on visual inspection of note shapes in spectrograms (Fig. 2) and comparisons of acoustic measurements. Other song types, however, showed some similarities in their notes and measurements and were therefore placed into seven groups for further statistical analyses. For each of these seven song groupings, we used principal components analysis to compare the five measured song features among males. The majority of variation in these datasets was explained by one or two of the first two principal components (see online supplement). Using the eigenvalues from these analyses, we plotted values for the first two principal components and then plotted 95% confidence ellipses around the points for each bird, using the package "ellipse" (Murdock and Chow 2007) in the R statistical program (R Foundation for Statistical Computing, Vienna, Austria). We considered birds with overlapping ellipses to have the same song types and those whose ellipses did not overlap to have different song types.

To determine if song sharing was more or less common between birds with adjacent territories (neighbors), we compared levels of song type sharing between neighbors to those between non-neighboring birds. We considered birds neighbors if they were observed singing at locations within 100 m of each other. For each pair of birds, we calculated an index of repertoire sharing (RS) using the formula $RS = Z/[(X + Y) - Z]$, in which X and Y represent the number of song types identified in each bird and Z represents the number of song types shared by the two birds (Hultsch and Todt 1981). This index potentially varied between 0, in which no songs are shared, and 1, in which all song types are shared, and it accounted for the fact that different males had different numbers of identified song types. We compared overall levels of song type sharing as well as sharing of first category and second category song types using independent samples *t*-tests. We further compared mean levels of sharing with neighbors and with non-neighbors by each male using a paired-samples *t*-test.

RESULTS

Singing Characteristics.—In our sample of 1,345 songs from 12 Pine Warblers, we initially identified 37 song types. Song repertoire sizes varied from 1–5 song types per male (mean = 3.08, SE = 0.42 song types) (Table 1). However, repertoire size was significantly influenced by number of songs sampled (ANOVA; $F_{1,10} = 11.33$, $P = 0.007$), indicating that our samples of at least some individuals were not large enough to accurately represent complete song type repertoires. Mean song characteristics at our two study locations, UMBS and COP, were not significantly different (in *t*-tests: $P > 0.1$) (Table 2).

Birds sang throughout the day, often while foraging 10–20 m above the ground in stands of red or white pine. Singers rarely stayed on one perch for long, typically moving from branch to branch at regular intervals between every few songs. We occasionally observed males singing while holding insect prey in their bills. Males and females were rarely seen together in the morning, whereas, they were often seen foraging near each other in the mid and late afternoon. Neighboring males appeared to counter-sing regularly, especially early in the morning, usually in alter-

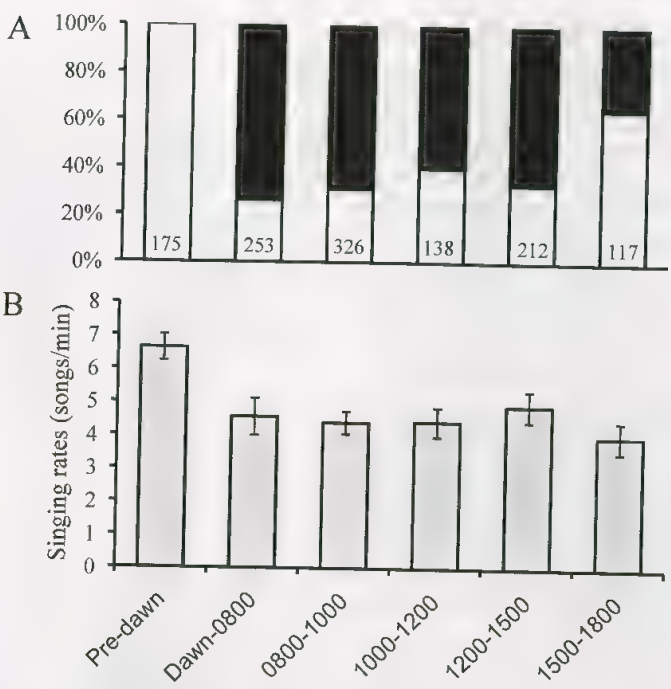

FIG. 3. (A) Proportions of time spent singing in repeat mode (black) and mixed mode (white) during each time period, with numbers of recorded songs shown at the base of each column. All songs produced before dawn were presented in mixed mode, whereas singing after dawn and during much of the day included mostly repeat mode singing. (B) Mean (± SE) singing rates (songs/min) during each time period, which were higher during pre-dawn singing than during the rest of the day.

but sometimes one male's song would overlap the song of a neighbor.

Songs recorded before dawn were always produced in mixed mode. Singing after dawn and during the rest of the day included mostly repeat mode, intermixed with bouts of mixed-mode singing (Fig. 3A). Birds appeared to sing with more variety later in the afternoon. Average singing rates were also significantly higher during the period before dawn (6.63 ± 0.39 songs/min) than during other times of day (4.48 ± 0.20 songs/min; *t*-test: $t_{86} = 4.74$, $P < 0.001$) (Fig. 3B).

Most Pine Warblers in our population had just one song type that they repeated for long stretches of time during daylight hours. We designated this song type as each male's first category song (Spector 1992). Other song types were only presented in alternation with other song types and were designated as second category songs. One male did not fit this pattern and had two song types that were sung in repeat mode on different occasions, both of which we scored as his first category songs. First category song types were sometimes included in bouts sung in mixed mode (19.1 ± 5.8% of the time), including singing bouts before dawn. Second category song types, in contrast, were never sung in repeat mode. Of the five most poorly sampled males (24–66 recorded songs, Table 1), three produced only one song type each in our recordings, which we scored as first category song, and one male had no recordings of 10 or more songs and thus could not be scored.

Occasionally (5.28% of songs recorded), a bird combined two of its song types into one continuous song, as noted by Rodewald et al. (1999), in which one trilled syllable was immediately followed by another at a slightly different frequency and rate (Fig. 2E). Four males exhibited such double songs (Table 1), which we scored as examples of mixed-mode singing, and three of these males produced multiple types of double songs using more than one combination of song types. Double songs occurred during all time periods, including before dawn, and could include either first or second category song types.

Approximately 30% of the examples we recorded included a first category song type.

Vocal Performance.—Frequency bandwidths of song types were significantly negatively related to trill rate in a linear regression (ANOVA: $F_{1,35} = 24.7$, $r^2 = 0.41$, $P < 0.001$), and the upper-bound regression line estimating the performance maximum for the population had a significantly negative slope ($y = -0.079x + 3.88$; $F_{1,5} = 69.6$, $r^2 = 0.93$, $P < 0.001$) (Fig. 4A). First category song types had significantly faster trill rates than did second category songs (*t*-test: $t_{35} = 2.64$, $P = 0.012$), but frequency bandwidths did not differ ($t_{35} = -0.625$, $P = 0.54$). Moreover, first category song types appeared closer on average to the upper performance limit than did second category songs (Fig. 4B), and this difference in orthogonal distance from the upper-bound line was nearly significant ($t_{35} = -1.879$, $P = 0.069$). A paired-samples *t*-test using a smaller sample of males exhibiting both song categories ($n = 8$) found no significant difference in the performance characteristics of each male's first and second category song types ($t_7 = -0.654$, $P = 0.53$). However, first category song types nearly always exhibited the highest trill rate in each male's repertoire (mean ± SE = 17.25 ± 1.66 notes/sec for first category song and 11.62 ± 0.83 notes/sec for second category song; $t_7 = 3.416$, $P = 0.011$).

Song Type Sharing.—Pair-wise comparisons between recorded males revealed that all males shared at least one song type with another male in the population, but no two males shared more than one song type. Of the 37 song types initially identified, many were shared among males and only 26 were structurally distinct across the population according to PCA. Males shared song types with 1–5 other males (mean = 2.5, SE = 0.4), including two song types that were shared between the UMBS and COP populations. Average levels of repertoire sharing between neighbors (RS = 0.067 ± 0.28) and non-neighbors (RS = 0.068 ± 0.26) did not differ overall ($t_{64} = -0.015$, $P = 0.99$) or in a paired-samples test ($t_{10} = 5.86$, $P = 0.57$) (Fig. 5). Furthermore, the mean proportion of first category songs that were shared between birds (33.3%) was not significantly different from the proportion of second category songs that were shared (36.1%; *G*-test: $G = 0.396$, df = 1, $P = 0.53$). In five cases, a song type used by one male as first category song was used by another as a second category song, and three males used the same song type as their first category song.

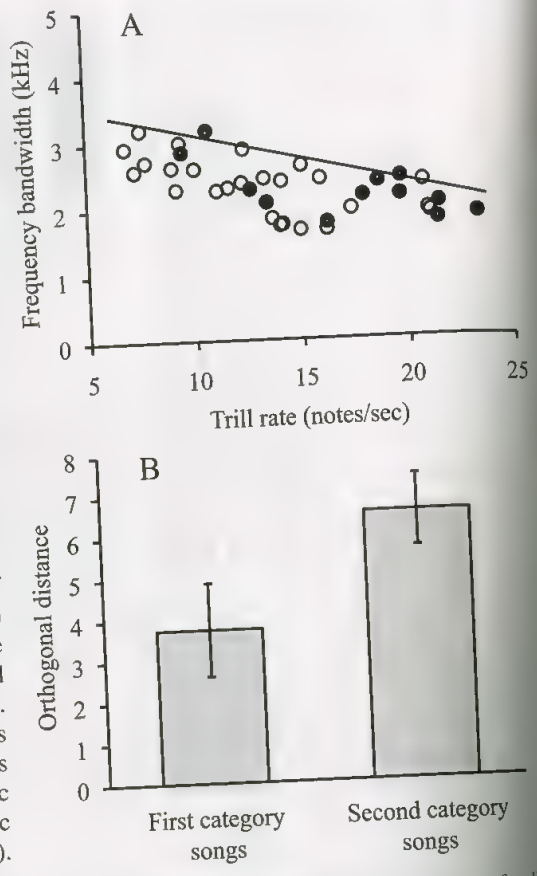

FIG. 4. (A) Frequency bandwidth versus trill rate for all song types recorded in the study ($n = 37$). An upper-bound regression line estimates the performance maximum for the population. First category songs (black filled circles) had significantly higher trill rates than did second category songs (white filled circles). (B) Mean (± SE) orthogonal distances from the upper-bound regression suggest that first category song types were performed closer to the performance maximum (i.e., had higher performance levels) than were second category song types.

DISCUSSION

In several respects, the singing patterns of Pine Warblers resemble those of other *Setophaga* wood-warblers. Like previously studied congeners, Pine Warblers exhibit a two-category song system in which one song type is typically repeated for long periods of time with high stereotypy (first category song) and other song types are mixed in irregular sequence during singing bouts (second category song) (Spector 1992). Songs before dawn were always sung in mixed mode, and pre-dawn singing occurred at significantly higher rates than did singing during

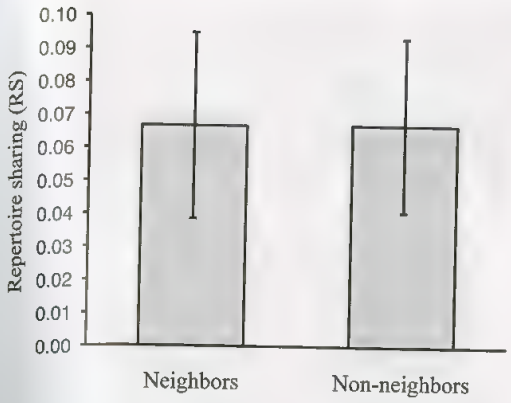

FIG. 5. Mean (± SE) levels of repertoire sharing between neighboring (n = 10) and non-neighboring (n = 56) males.

the rest of the day. Furthermore, and perhaps most interestingly, first category song types exhibited higher performance characteristics (e.g., higher trill rates) than did second category songs, suggesting that first category song types are generally more challenging to perform (Ballentine et al. 2004, Beebee 2004b). Nevertheless, as has been shown in several other wood-warbler species (Lemon et al. 1985; Staicer 1989; Spector 1991, 1992; Beebee 2002, 2004b), the particular song types used in each category were not standardized across males in our population. First category song types of some males were nearly identical to the second category song types of other males. Our results are consistent with Beebee's (2004b) suggestion that individual males subdivide their repertoires into two distinct singing categories in order to highlight a particularly well-performed song type.

Pine Warblers also exhibit several interesting differences from other wood-warblers, as noted by previous authors. For instance, Spector (1992) noted that Pine Warblers regularly produce more than one song type in alternation during daytime singing, unlike most congeners. Our study confirms this observation by showing that >25% of song bouts throughout the day included multiple song types produced in mixed mode (Fig. 3A). However, we should note that our study was conducted relatively late in the breeding season, and other wood-warbler species are known to produce first category songs less frequently after mating (e.g., Spector 1991); consequently, it is possible that the high levels of second category singing we observed in our population do not reflect typical singing patterns during breeding. Future investigations should confirm whether frequent second category singing during daylight is indeed typical of Pine Warblers throughout the year, as implied by previous authors (Spector 1992, Rodewald et al. 1999), or occurs only during the later part of the breeding season.

Unlike other wood-warblers, Pine Warblers regularly included their first category song types in bouts sung in mixed mode (<20% of the time), including singing bouts before dawn. Of the nine males in our study from which we recorded more than one song type, all were observed mixing their first and second category song types during singing bouts. For comparison, Spector (1991) reported only a single Yellow Warbler (out of 17 study subjects) that interspersed its first category song with second category song types during predawn singing bouts. Pine Warblers are also unusual in producing double songs, in which two song types are concatenated into one continuous song. As in other examples of mixed-mode singing in this species, double songs sometimes included a mixture of first and second category song types. Whether or not these combined songs have a specialized function in communication remains to be investigated.

In general, the two-mode song system of Pine Warblers appears to lack the clear distinction between song categories typical of most other *Setophaga* wood-warblers (Spector 1992). Yet, in Pine Warblers these song categories nevertheless exhibited consistently different acoustic characteristics, as in other taxa (Spector 1991, Staicer 1996, Beebee 2004b). First category songs had significantly higher trill rates than did second category songs. Furthermore, in comparisons to a performance maximum for the population estimated by plotting trill rates against frequency bandwidths, first category songs were generally closer to this upper limit (Fig. 4), although not significantly so (P = 0.069). In a similar comparison of vocal performance levels in Yellow Warblers, Beebee (2004b) showed that first category song types were significantly closer to a performance maximum than were second category song types when inter-individual variation was controlled for using paired-samples comparisons (n = 33). Our paired-samples analysis using a much smaller sample of Pine Warblers (n = 8) showed no significant differences in this measure of vocal performance. Yet, within each male's repertoire, first category song types nearly always exhibited the highest trill

rates. Trill rates could be an especially salient indicator of vocal performance in Pine Warblers, unlike frequency characteristics which can degrade during transmission and thus might provide less reliable information in long distance communication (Wiley and Richards 1982).

Pine Warblers also differ from previously studied taxa in their patterns of song type sharing among males. Unlike Yellow Warblers (Beebee 2002) and Chestnut-sided Warblers (Byers 1996), which preferentially share second category song types with close neighbors, Pine Warblers do not appear to share song types with neighbors over non-neighboring males. Indeed, our subjects shared song types between the two study populations, approximately 100 km apart, just as often as they did between adjacent territories, and levels of sharing did not differ between first and second category songs. In other wood-warbler species, second category song is thought to be used primarily during territorial interactions (Spector 1992, Wiley et al. 1994, Byers 1995), and it has been suggested that song type sharing allows complex communication between neighboring males (Beebee 2002, Catchpole and Slater 2008). Yet, studies suggest that male wood-warblers do not use their shared and unshared songs differently during territorial interactions (Lemon et al. 1985, Byers 1996), and playback experiments show that males often use first rather than second category song when responding to potential territorial intruders (Beebee 2004a). Thus, an alternative explanation for song type sharing is that it is simply a consequence of how males learn their songs (Spector 1992, Beebee 2002), with males preferentially learning some of their second category song types from neighbors following natal dispersal. Therefore, song sharing might have no relevance to how males use their songs to interact with other males (Beebee 2004a).

If general patterns of song type sharing in wood-warblers are explained by learning rather than their functional significance in communication, the absence of any clear relationship between song sharing and geographic distance in our Michigan population of Pine Warblers would suggest that these birds have different vocal learning patterns than most congeners. This might make sense, as Pine Warblers are among the few songbirds that sing year-round, including during migration (Rodewald et al. 1999), so young birds are presumably frequently exposed to song types from wide geographic areas. Some more southerly populations of Pine Warblers are known to be non-migratory (Rodewald et al. 1999), and it would be interesting to compare the patterns of song type sharing in our population to those of year-round resident birds. Levels of song sharing with immediate neighbors, as well as song repertoire sizes, might be greater in resident populations (Ewert and Kroodsma 1994).

Although the two song categories of wood-warblers may not have distinct sex-specific functions as previously thought (Beebee 2004a), differences in their acoustic characteristics and patterns of use nonetheless suggest that they play different roles in communication. For instance, the higher performance characteristics of first category songs might reflect the role that these song types play as assessment signals (Beebee 2004b), unlike second category singing which may have functions in mediating interactions between territorial males. Assessment signals presumably could be directed at either male or female receivers, which is consistent with previous findings that males tend to use their first category songs in the contexts of both attracting females and repelling perceived male intruders (e.g., Spector 1991, 1992; Wiley et al. 1994; Bolsinger 2000; Beebee 2004a). Song categories may also have evolved as specializations for communication over different distances and under different levels of noise (Wiley et al. 1994). Repeating a signal with high redundancy and stereotypy, as in first category singing, is a common adaptation for overcoming signal degradation and background noise when communicating over long distances (Wiley and Richards 1982, Wiley 1994). Repetition of a signal allows listeners more opportunities for detecting and assessing signal features (Byers 2007, Price 2013). In contrast, there should be relatively little selection for such redundancy in signals used at closer range and between familiar individuals, such as territorial neighbors. Future studies should investigate these possibilities in Pine Warblers and in other wood-warbler taxa, perhaps using playback experiments (Beebee 2004a). Our descriptive analysis presented here provides an important step towards understanding the evolution and function of two-category song systems.

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NEST PREDATION IN AN ANTHROPOGENIC LANDSCAPE

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ABSTRACT.—Wood Thrushes (*Hylocichla mustelina*) are experiencing widespread population declines. Knowing the relative contribution of predator species to overall rates of nest predation of Wood Thrushes, and understanding how the thrushes are affected by temporal and landscape factors, may be important elements in choosing and devising effective management strategies. We used miniature video cameras to identify nest predators of Wood Thrushes in a highly fragmented landscape in Ontario. Eleven species of birds and mammals were recorded as nest predators. Birds accounted for almost twice as many predation events as mammals, and three species – Brown-headed Cowbird (*Molothrus ater*), Cooper's Hawk (*Accipiter cooperii*), and raccoon (*Procyon lotor*) – accounted for the majority. Species such as American Crow (*Corvus brachyrynchos*), Blue Jay (*Cyanocitta cristata*), eastern gray squirrel (*Sciurus carolinensis*), and Common Grackle (*Quiscalus quiscula*) that are often speculated to be important nest predators in agricultural and suburban landscapes contributed little or nothing to overall predation rates. We tested hypotheses concerning effects of nest stage, time of nesting season, forest size, forest cover, urban housing pressure, and prior predation events at a nest on the probability of nest predation. Our models showed only two of these factors to be significant: prior predation at a nest increased the chance of a subsequent predation event and increasing the measure of urban pressure reduced the chance of a predation event. The many alternate and easy food sources associated with humans might divert the attention of potential predators from nesting birds in urban forests. *Received 19 October 2012. Accepted 19 April 2013.*

Key words: accipiters, brood parasitism, landscape effects, nest predation, raccoons, urbanization, Wood Thrush.

Increased nest predation is often associated with changes in landscape features such as a reduction in regional forest cover (Donovan et al. 1995), a decrease in forest size (Small and Hunter 1988), and an increase in the number of houses in and around a forest (Wilcove 1985, Phillips et al. 2005, Sinclair et al. 2005), presumably because the modified urban landscape can support a far greater abundance of predators compared to rural landscapes. Raccoons (*Procyon lotor*), for example, are important nest predators (Pietz and Granfors 2000, Renfrew and Ribic 2003) and maintain much higher population densities in urban than in rural areas (Danielson et al. 1997). Temporal factors such as the time of season (date) and stage of nest cycle can also affect rates of nest predation: nest predation can decrease as the breeding season progresses (Burhans et al. 2002) and can be higher in the nestling stage than during incubation (Peak et al. 2004, Cottam et al. 2009). Multiple predation events at the same nest on different days by one or more predator species can occur (Stake et al. 2004), but it is unknown whether a prior predation event at a nest increases the likelihood of a subsequent predation event.

Beginning in 2006, we used miniature digital video cameras, equipped with infrared illumination that permitted recording at night as well as day, to document predators at nests of Wood Thrushes (*Hylocichla mustelina*) in forests situated in a highly fragmented landscape in southern Ontario. We had several objectives. First, we wished to identify region-specific nest predators in order to gain a better understanding of their relative contribution to overall rates of predation near the northern edge of the Wood Thrush's breeding range in North America. Second, despite the multitude of nest survival studies published in the past twenty years, large knowledge gaps still remain in our understanding of spatial and temporal variation in which species contribute most to nest predation rates for songbirds. We therefore tested hypotheses concerning effects of nest stage, time of nesting season, forest size, forest cover, urban housing pressure, and prior predation events at a nest on the probability of nest predation. We predicted predation risk would be different during the incubation and nestling stages. We expected that predation pressures would be different between the early nesting season and the late nesting season. We predicted that predation rates would differ between small forests and large ones, in landscapes with low forest cover and those with high forest cover, and in forests with low

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housing intensity and those with high housing intensity. Finally, we hypothesized that predation rates would be different at nests that had experienced a prior predation event than those without any predation history.

METHODS

Data Collection.—We conducted field work during 2006–2010 in 14 woodlots in the Region of Waterloo, Ontario (population 553,000; 2011 estimate, www.regionofwaterloo.ca), which encompasses a 1,369 km^2 area in southwestern Ontario. The study sites consisted of upland deciduous forest and were located in an agricultural/urban-suburban landscape with 14% forest cover and a mean forest patch size of 12.8 ha (see Friesen et al. 1999 for additional landscape details). Thirteen study sites ranged in size from 2–31 ha, with the fourteenth being 136 ha. Five sites were closely grouped and separated from one another by 60–500 m; the other sites were distributed broadly across the Region of Waterloo. Nests were located from early May to early August using sound playbacks combined with systematic search and behavioral cues.

We used two miniature infrared video cameras and digital-recorder systems (Sentinel ELF™ 24 Digital Video Recording System, Sandpiper Technologies, Inc., Manteca, California, USA; and WildEye™, Warner Bay Company, Waterloo, Ontario, Canada) to monitor nests. Four camera and recorder systems were used from 2006 to 2008 and six systems in 2009 and 2010. Whenever possible, we installed cameras at newly built nests where egg-laying had not yet commenced or where the host clutch was not yet complete (two eggs or fewer). We also used nests that were further advanced in the incubation or nestling stages. Cameras were positioned within 100 cm of a nest because of the limited illumination provided by infrared lighting at night. Each camera was covered in camouflage tape and attached to a similarly camouflaged telescopic pole that was hollow and fitted over an anchoring metal insert. The digital recorder and accompanying battery were in a camouflaged case stowed 25–40 m from the camera. We exchanged digital recorders and batteries daily, and monitored the nest contents using a remote video monitor or manually with a telescoping pole and mirror if recording problems had occurred. Recorded footage was reviewed daily as necessary to confirm the nest's fate and to account for missing nest contents. Cameras were operated until the nest failed or young were fledged.

We defined a predation event as one in which one or more eggs and/or nestlings were removed by an individual predator species in a 24-hr interval. For example, the removal of two eggs singly in two trips over a period of 25 mins on one day by an eastern chipmunk (*Tamias striatus*) was considered one event. By contrast, the removal of two eggs, one each by a chipmunk and a Blue Jay (*Cyanocitta cristata*) on a single day, was considered two events. A single nest could therefore experience more than one predation event. We considered forced fledging (i.e., if the presence of a predator induced one or more nestlings to depart the nest prematurely) to be a predation event (Stake et al. 2004).

Analysis.—We used logistic regression (McCullagh and Nelder 1983) to model the probability of one or more predation events on any observation day as a function of the following explanatory variables:

- Nest stage: whether the nest held eggs or chicks.
- Nest period: whether nest monitoring began before Jun 15 in any year (this date marks the approximate beginning of the start of second nesting attempts by Wood Thrushes in our area (Friesen et al. 2000).
- Forest size: the area of the forest patch where the nest was found. We did not consider using forest edge as a variable because our woodlots were so small that they could all be considered to consist essentially of edge habitat (Friesen et al. 1999).
- Urban pressure (UP): a measure of the intensity of human habitation within a circle centered on the nest at various radii (see below).
- Percent forest cover (PCFC): the percentage of forest cover within a circle, centered on the nest at various radii (see below).
- Prior predation: whether the nest had suffered one or more predation events on an earlier observation day.

We considered existing methods for quantifying exposure to urban pressure (Rodewald and Shustack 2008) to be rather arbitrary and too insensitive to spatial variation to be suitable for our purpose. We treated urban pressure as a continuum of uncertain dimensions, which should be as carefully estimated as other parameters in our study. We chose to evaluate the urban

FIG. 1. Urban Pressure (UP) at three Wood Thrush nests labelled A, B, and C using a radius (D) of 800 m. The UP at these nests was A: 0.12, B: 0.35 and C: 2.37. Nests in 2010 are shown as stars and houses as squares (representing points). The footprints of institutional and commercial buildings are also shown, as are wooded areas outside the study area.

environment using single family dwellings, as these account for over 90% of the urban fabric within our study area and are implicated in most hypotheses regarding the impact of urban-sensitive birds (Friesen et al. 1995, Mancke and Gavin 2000). Each dwelling unit within 4 km of each nest was mapped and given metric coordinates, as well as estimated occupancy and demolition dates (where applicable). Four km is well beyond the distance where (based on an exploratory analysis) we expected to see the greatest impacts of urbanization, and because many of our nests are much more closely spaced than this, autocorrelation would be expected to become the predominant consideration.

Merely counting the number of houses that fall within a given radius produces an index with a strong bias toward the outer edge of the circle, as a result of the exponentially increasing area under evaluation. This suggests that the urban units should be inversely weighted by their squared distance from the nest. However, aggregating the inverse distance does not entirely eliminate the problem of the excessive contribution of the outer edge, and it also introduces a new one: houses very close to the nest tend to overwhelm the aggregate score.

We developed a simple, generalized method to overcome both of these problems. AMID (Aggregate Modified Inverse Distance) used the distance variable 'D' to describe the radius of the evaluation area in two additional ways. First, it was used to limit the excessive influence of units that were close to the point of origin—the nests in this study—by adding the constant 2D to the individual squares of the distance between nest and dwellings. A second constant (2+D) was then subtracted from the modified inverse distances so that, at D, the contribution of the units being aggregated was reduced to zero. For any nest:

$$AMID = \sum_j \left[\frac{D}{d_j^2 + 2D} - \frac{1}{2+D} \right]$$

where d_j is the distance between the nest and house j and the sum is over all houses within a circle of radius D centered at the nest (Fig. 1).

We used Microsoft Access to implement AMID as SQL statements involving a cross join (Cartesian product) of a table of nests and another of dwellings, with values for D ranging over 11 values from 125–4,000 m. The values generated by AMID were not standardized across D

TABLE 1. Wood Thrush nest predator events video-recorded in the Region of Waterloo, Ontario, 2006–2010.

Predator species	Incubation	Nestling	Total
Brown-headed Cowbird (*Molothrus ater*)	15		15
Raccoon (*Procyon lotor*)	3	7	10
Cooper's Hawk (*Accipiter cooperii*)		9	9
American Crow (*Corvus brachyrynchos*)	4	1	5
Blue Jay (*Cyanocitta cristata*)	4		4
Red Squirrel (*Tamiasciurus hudsonicus*)	2	2	4
Eastern Chipmunk (*Tamias striatus*)	2	1	3
Eastern Gray Squirrel (*Sciurus carolinensis*)		2	2
Red-tailed Hawk (*Buteo jamaicensis*)		2	2
Sharp-shinned Hawk (*A. striatus*)		1	1
Short-tailed Weasel (*Mustela erminea*)		1	1

therefore, direct comparisons were made only among nests for a given value of D. Forest sizes and the percentage of forest cover (PCFC) surrounding each depredated nest were measured using digital forest cover mapping, created from 2006 aerial imagery (accessible via Google Earth; www.earth.google.com) at a scale of approximately 1:5,000.

Using the statistical package R (R Core Development Team 2005) and the GLM function, we modelled the probability of one or more predation events on any observation day as a linear function of the explanatory variables on the logistic scale. We investigated a variety of models, each with only one measure of UP and PCFC. All predation events were grouped, as our sample size was too small to consider predator subsets excepting the Brown-headed Cowbird (*Molothrus ater*). The analysis was repeated using predation by cowbirds and included only observation days when eggs were in the nest. As well, we analyzed predation by mammals and birds other than cowbirds separately. In these analyses, nests with other predation events were treated as censored on the day of the event. Data were pooled across years and across study sites because of small sample sizes.

To select an appropriate scale for urban pressure and percent forest cover in the models, we followed an exploratory process similar to the one described in Grand et al. (2004). Including all other explanatory variables in the model, we varied the value of D over an 11 × 11 grid and selected the scales for UP and PFC that gave the lowest *P*-value. By construction, there is high correlation between the UP (and PCFC) variables for values of D that are close together. We also explored adding a second UP or PCFC measure after the initial selection. None of these additions improved the fit of the model significantly.

RESULTS

We video-monitored 86 nests for 1,289 observation days (614 incubation days, 675 nestling days) and recorded 56 predation events at 42 nests (Table 1). Eight nests were depredated twice, by the same predator species at five nests and by two different species at three nests. Three nests were each depredated three times by two different species. Three nests were partially depredated during the incubation stage but each went on to fledge at least two nestlings. No adult females were depredated on the nest during the study. Birds were responsible for 64% of the predation events at nests, divided among non-raptorial birds (n = 24 events) and raptors (n = 12 events).

Three species contributed to the majority (61%) of predation events (Table 1). Brown-headed Cowbirds were the most frequently recorded predators (n = 15 events, all in the incubation stage). Thirteen cowbird predation events occurred within the first several days of the incubation stage and involved the removal or puncture of one or two host eggs. Two other cowbird predations occurred later in the incubation stage, one event involving the destruction of an entire clutch of three host eggs that were ≥7 days old and another event involving the removal of two of three host eggs that were 11 days old, causing the female thrush to abandon the nest. Raccoons were the second most frequently recorded predator (n = 10 events, three in the incubation stage and seven in the nestling stage), followed by Cooper's Hawks (*Accipiter cooperii*) (n = 9 events, all in the nestling stage).

In all of the models considered, whether or not a nest had suffered prior predation had a strong

TABLE 2. Logistic regression modelling of factors affecting observation days at nests of Wood Thrushes in Ontario with one or more predation events.

Coefficient	Estimate	Standard error	*P*-value
Intercept	−4.32	0.85	< 0.001
Nest stage	−0.20	0.29	0.50
Nest period	0.43	0.31	0.16
Forest size	0.01	0.004	0.19
Urban Pressure 800-m radius	−3.23	1.33	0.015
Percent forest cover 500-m radius	−0.03	0.015	0.082
Prior predation	2.14	0.38	< 0.001

effect on the chance of subsequent predation. The *P*-value for UP was a minimum for a radius of 800 m. For this model, summarized in Table 2, the null deviance was 454.59 on 1,288 degrees of freedom, the residual deviance was 404.58 with 1,282 degrees of freedom, and the AIC value was 4.18. In the model, increasing the measure of urban pressure at 800 m significantly reduced the chance of a predation event, all else being held constant. We saw similar significance levels as the radius of the circle used to determine the urban pressure measure increased. As we decreased the radius, the effect of urban pressure became marginally significant. For no value of D was the effect of PFC significantly different from 0. We also considered models with two values for urban pressure and percent forest cover at various scales. None of these models fit the data as well according to the AIC criterion.

Because of how urban pressure was defined, the strength of the effect of UP on daily survival rate was not apparent. In our data set of 84 nests, UP at 800 m varied from 0 to 4 with the distribution highly skewed. Most values were between 0 and 1. The estimated effect was −3.23 and the probability of a predation event on any particular day was small. An increase in UP of 1 unit reduced the relative risk of daily predation by a factor of ~30, all else being equal. Because of the exploratory nature of the analysis, we may have overestimated the effect of UP.

We repeated the above modeling exercise considering only predation events by Brown-headed Cowbirds. The data were filtered to include only observation days when eggs were in the nest. None of the explanatory variables had a significant effect over a wide range of possible models achieved by varying the radius of the circle used for calculating the urban pressure and percent forest cover. We also tried to fit similar models for avian predation events (other than those by cowbirds) and mammalian predation events. Perhaps because of the small sample sizes, we were not successful in detecting any significant effects.

DISCUSSION

Eleven predator species – six of them avian and five mammalian – depredated nests of Wood Thrushes in our study. Birds were responsible for almost twice as many predation events as mammals (64 vs. 36% respectively). By contrast, video surveillance studies conducted in fragmented forests in the United States reported a relatively even mix of snakes, birds, and mammals as predators of eggs and nestlings (Thompson 2007). We did not detect snakes at nests, although they have been confirmed as important nest predators at more southerly latitudes (Stake et al. 2004, Benson et al. 2010). The black rat snake (*Elaphe obsoleta*) in particular has been identified as a nest predator throughout its range but is extremely uncommon in southern Ontario (COSEWIC 2007) and is not known to occur in the Waterloo region.

Human-associated predators typical of fragmented landscapes predominated in our area. A wide variety of human-adapted species is often speculated to operate as co-dominant nest predators in urban and fragmented landscapes (Environment Canada 2007). In our case, three species – Brown-headed Cowbird, raccoon, and Cooper's Hawk – accounted for the majority of predation events (Table 1). This pattern is similar to those observed elsewhere where a small subset of potential nest predators was responsible for most of the predation (Benson et al. 2010, Cox et al. 2012). Absent from our predator list were species such as Common Grackle (*Quiscalus quiscula*) that were abundant at our study sites and that is considered to be an important nest predator

(Wilcove 1985, Reed and Elphick 2001). Blue Jays and American Crows (*Corvus brachyrynchos*), two species labeled as major "nest robbers" (Mancke and Gavin 2000), were common at our sites, yet together contributed to only 16% of predation events. Eastern gray squirrels (*Sciurus carolinensis*), another presumed nest predator (Kluza et al. 2000), were also abundant and although we recorded two instances of them precipitating premature fledging, they were never observed consuming eggs or nestlings, contrary to what we witnessed for eastern chipmunks and red squirrels (*Tamiasciurus hudsonicus*). Our study provides further evidence that the abundance of a potential nest predator species does not automatically equate to actual risk of predation for a songbird species, and that the cast of species regularly identified as common nest predators in urban and fragmented habitats may require revision with respect to their individual importance.

Raptors, particularly accipiters, were frequently observed predators at our study sites, and all their predations involved nestlings. Unlike the two other major predators in this study, Cooper's Hawks (along with the other raptors) were recorded only in the rural study sites, which is surprising given that the species has become locally common in many urban centers in Ontario (Gahbauer 2007). Accipiter populations have increased significantly in Ontario in recent decades (Cadman et al. 2007), and they may be re-emerging as major nest predators.

Accipiters appeared to visit nests to monitor the growth of potential prey (see also Cox et al. 2012). Cooper's Hawks made multiple visits to two nests during both the incubation and early nestling stages but removed nothing from the nests until the nestlings were at least 6 days old. This is a risky 'farming' strategy for them because although if successful it maximizes their reward, it could also mean failure if the nest is found by other predators. At two nests depredated by Cooper's Hawks, host nestlings demonstrated remarkable survival instincts: two thrush chicks in each nest, aged 9–10 days, jumped out within 3 mins of the departure of a hawk with a nestling; we could not determine the ultimate fate of these precocious nestlings.

We found support for effects of prior predation events on the probability of predation, as a second (or third) event on any observation day following an initial predation was significantly more likely. Eleven of the 42 depredated nests experienced multiple predation events. Some of these likely involved single individuals making repeat visits to nests, although this wasn't always an obvious conclusion because the interval between successive predation events ranged from 1–5 days. Six nests were depredated by two different predator species, suggesting that these nests may have been more conspicuous or vulnerable in some manner.

Contrary to our prediction, we found support for effects of higher levels of urban pressure reducing the probability of predation. It is often hypothesized that urban and suburban environments support a greater abundance of generalist and opportunistic nest predators that in turn greatly increase the risk of songbird nest predation (Wilcove 1985, Kluza et al. 2000). In our case, the reverse was true: as housing intensity increased in and around a nest site, the chance of a predation event decreased. Reduced nest predation in urban environments has been reported for several other urban species (Burhans and Thompson 2006, Rodewald and Shustack 2008). This pattern suggests there may be some prophylactic effect of urban development on songbird nests; perhaps there are so many alternate and easy food sources associated with houses that potential predators such as raccoons, crows, and jays, though abundant in urban settings, do not pay great attention to nests (Stracey 2011).

Higher rates of brood parasitism have been reported in urban than in rural landscapes (Phillips et al. 2005, Burhans and Thompson 2006, Rodewald and Shustack 2008), but we found that the probability of cowbird predation events was unaffected by urban pressure or any of the other measures included in our models. The destruction of two unparasitized nests by cowbirds late in the incubation stage might have been manifestations of "farming tactics" to create additional opportunities for parasitism (Hoover and Robinson 2007). Unfortunately, neither of the two female thrushes involved was banded so it was not possible to know if they re-nested and were subsequently parasitized.

The probability of predation in our study area was unaffected by forest size or percent forest cover. Such lack of influence could be attributed to the fact that all our woodlots were of relatively small size and that regional forest cover was so low that any possibility of meaningful association became irrelevant as larger radii were used in the models. We also found that nesting period or

nesting stage did not affect the probability of predation. Predation events were almost evenly split between the incubation and nesting stages (54 vs. 46% respectively). Of the three most dominant predators in our study, one depredated nests only during incubation, another only during the nestling stage, and the third depredated in both stages (Table 1), all of which effectively neutralized any association between nesting stage and probability of nest predation.

Populations of Wood Thrushes have undergone significant decline across their North American breeding range. In Canada, the species was recently assessed as 'Threatened' by the Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2012). The reasons for the species' population decline are not clearly known. However, nest predation is an important factor in passerine ecology (Thompson 2007). Knowing the identity of predators of Wood Thrushes and their relative contribution to predation levels may be an important element in choosing and devising successful management strategies for the species.

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NEST-SITE SELECTION, NEST SURVIVAL, PRODUCTIVITY, AND SURVIVAL OF SPRUCE GROUSE IN WISCONSIN

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ABSTRACT.—Spruce Grouse (*Falcipennis canadensis*) are listed as threatened in Wisconsin, and the boreal habitats in which they occur are likely to be threatened by changing climatic conditions. However, the limited information available on Spruce Grouse in the Upper Great Lakes region makes it unclear which habitat features are important for Spruce Grouse nesting in Wisconsin. We radiotracked 30 female Spruce Grouse in northern Wisconsin from 2007–2012 and located 25 nests. Eighteen of 25 nests were beneath black spruce (*Picea mariana*) trees. Only three nests were in upland, and only one in a stand of jack pines (*Pinus banksiana*), in contrast to studies from Michigan and Ontario. Overall concealment was a good predictor of nest sites for Spruce Grouse, but not a good predictor of nest survival. Nest survival was associated with moderately dense and uniform 0–0.5 m lateral vegetation cover. Seventeen of 25 nests were successful, with a daily survival rate of 0.985, overall productivity of 1.0 young/female, and 1.9 young/successful nest. Annual survival of adult males was estimated at 54%, adult females at 40%, and juvenile survival at 14% and 24% by two different methods. Estimates of λ of 0.65 and 0.67 suggest a declining population, but the upper confidence limit exceeds 1, not ruling out a stable or slightly increasing population. Protecting black spruce swamps will protect important nesting habitat for Spruce Grouse in Wisconsin. *Received 18 October 2012. Accepted 3 May 2013.*

Key words: black spruce, concealment, *Falcipennis canadensis*, jack pine, nest survival, nest-site selection, Spruce Grouse, survival.

Nesting is a critical part of the annual cycle, and nest success is often an important component of population dynamics. Poor nest success can severely limit annual fecundity (Walankiewicz 2002, Peery et al. 2004). However, birds can improve the likelihood of nest survival by selecting nest sites that provide protection from predators and weather (Møller 1989, Heltzel and Earnst 2006), and various vegetative features have been linked to nest success (e.g., Martin and Roper 1988, Gregg et al. 1994, Warren et al. 2008). Because nest predation is often the biggest limit to reproductive success (Martin 1992), selecting safer nest sites can help mitigate effects of predation and as a result, nest-site selection can be a driver of habitat selection and life-history traits (Martin 1993). Understanding factors that influence nest-site selection and nest survival can aid managers in developing conservation strategies that maintain high-quality habitat for birds of conservation concern.

Spruce Grouse (*Falcipennis canadensis*) are threatened in Wisconsin (Wisconsin Department of Natural Resources 2011), yet little is known here about their behavior and ecology, and we are not aware of any previous reports of nests in the state. Prior to our work, only a few locations were known to host consistent populations of Spruce Grouse. Understanding habitat requirements in our area is critical, as Wisconsin is the southern range limit of Spruce Grouse, where productivity may be low (Whitcomb et al. 1996) and birds may be particularly vulnerable to extirpation because of patchy habitat (Fritz 1979, Bouta and Chambers 1990). Additionally, conifer species are predicted to recede northward because of global climate change, which will likely negatively impact conifer-associated boreal bird species (Scheller and Mladenoff 2005, Matthews et al. 2007, Prasad et al. 2007, Wisconsin Initiative on Climate Change Impacts 2011).

Rangewide, Spruce Grouse nest on the ground under a variety of conifer types. Stands of upland lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*) are used in Alberta (McCourt et al. 1973, Keppie and Herzog 1978, Redmond et al. 1982). In New Brunswick, Redmond et al. (1982) reported jack pine (*Pinus banksiana*), black and red spruce (*Picea mariana, P. rubens*), and balsam fir (*Abies balsamea*) to be the major nesting habitat types. Spruce Grouse use stands of black spruce and tamarack (*Larix laricina*) in Maine (Whitcomb et al. 1996), and use stands of black and white spruce in Alaska (Ellison 1971,

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In the Great Lakes region, Haas (1974) found Spruce Grouse nesting primarily in lowland black spruce swamps in Minnesota, but in Michigan and Ontario, birds were reported to use stands of upland jack pines (Robinson 1980, Naylor et al. 1988, D'Eon 1997). Pietz and Tester (1982) reported Spruce Grouse in Minnesota nesting in both upland jack pine and lowland tamarack and black spruce. Redmond et al. (1982) found differences in habitat, nest concealment, and nest success between eastern and western Spruce Grouse populations and cautioned against applying findings from one area across the entire range. Moreover, while studies from the eastern and western edges of the range have sampled >100 Spruce Grouse nests, the information available from neighboring states involves relatively few nests (Michigan, $n = 9$ [Robinson 1980]; Minnesota, $n = 12$ [Haas 1974], $n = 7$ [Pietz and Tester 1982]).

Because Spruce Grouse have been observed to nest in many different conifer habitat types, ranging from upland pine to lowland spruce swamp, and we had no information on Spruce Grouse nests in Wisconsin, an investigation of Spruce Grouse nest selection was needed to inform managers of important habitat features for Spruce Grouse nests. We used radiotelemetry to track female Spruce Grouse to nests, sampled vegetation at nests and paired random points, and used information-theoretic techniques to (1) differentiate Spruce Grouse nests from nearby randomly selected points and (2) examine habitat factors related to nest survival. We predicted variables related to greater vegetation density, ground cover, conifer cover, and concealment would best describe Spruce Grouse nest sites and be related to improved nest survival. Additionally, because threats to Spruce Grouse left us uncertain about demographic trends at our sites, we used data collected from telemetry visits to derive estimates of productivity, adult and juvenile survival, and the rate of increase of the population, λ.

METHODS

Study Areas.—We worked at two study areas in northern Wisconsin: in the west, on the Great Divide Ranger District of Chequamegon-Nicolet National Forest (CNNF) in Ashland, Bayfield, and Sawyer Counties (approx. 1,150 km^2); and in the east, Vilas County Forest (VCF) (approx. 160 km^2) and the Eagle River Landbase of CNNF (approx. 1,000 km^2) in Forest, Oneida, and Vilas counties (Fig. 1). Upland broadleaf forest types (48% of area) were common on CNNF, with black spruce, tamarack, and mixed conifer (black spruce, tamarack, and some northern white cedar [*Thuja occidentalis*]) swamps spread across the landscape (18%; CNNF reconnaissance data). Upland jack pine (1%) and red pine (*Pinus resinosa*; 6%) stands were scarce on CNNF (CNNF reconnaissance data). Upland broadleaf forest (43% of area) was also common on VCF, and black spruce and tamarack swamps (11%) were uncommon, but this site contained greater percentages of jack pine (13%) and red pine (10%) on the landscape (VCF reconnaissance data).

Radiotelemetry.—We located female Spruce Grouse by broadcasting a recording of the female cantus call (Boag and McKinnon 1982) and the male flutter-jump and tail-flick (Lumsden 1961) from a handheld speaker and small mp3 player. Females generally responded with a cantus, though in several instances we located silent birds (see Worland et al. 2009 for more on survey methods). We used 4.3–6.1 m telescoping noose poles (Zwickel and Bendell 1967) to capture female Spruce Grouse and fitted them with necklace-style radiocollars (Advanced Telemetry Systems [Isanti, MN] ATS A3950 [approx. 12.5 g when ready to mount] and Holohil [Carp, Ontario, Canada] RI-2D [approx. 9.3 g when ready to mount]). Beginning in fall 2010, we also banded eight birds with a 9.5 mm inside-diameter aluminum band and several wrap-around plastic colorbands. We tracked birds by homing using 3-element folding Yagi antennas and Telonics (Mesa, AZ) RA-23K H-antennas, and Communications Specialists (Orange, CA) R-1000 receivers and Advanced Telemetry Systems ATS R410 receivers.

Locating and Monitoring Nests and Grouse.—We tracked birds from 16 May 2007 to 10 July 2012, as part of a larger project to understand Spruce Grouse habitat use (Anich et al. in press). Frequency of tracking varied throughout the project, but was ~1 location point/week. When we first located an individual Spruce Grouse on a nest, we flushed it to estimate nest initiation date, and then flushed the hen only one additional time to determine full clutch size. We marked nest locations using a Global Positioning System (GPS) receiver and flagging tied ~10 m away from nests. During subsequent nest checks, we used radiotelemetry to determine if a hen was on

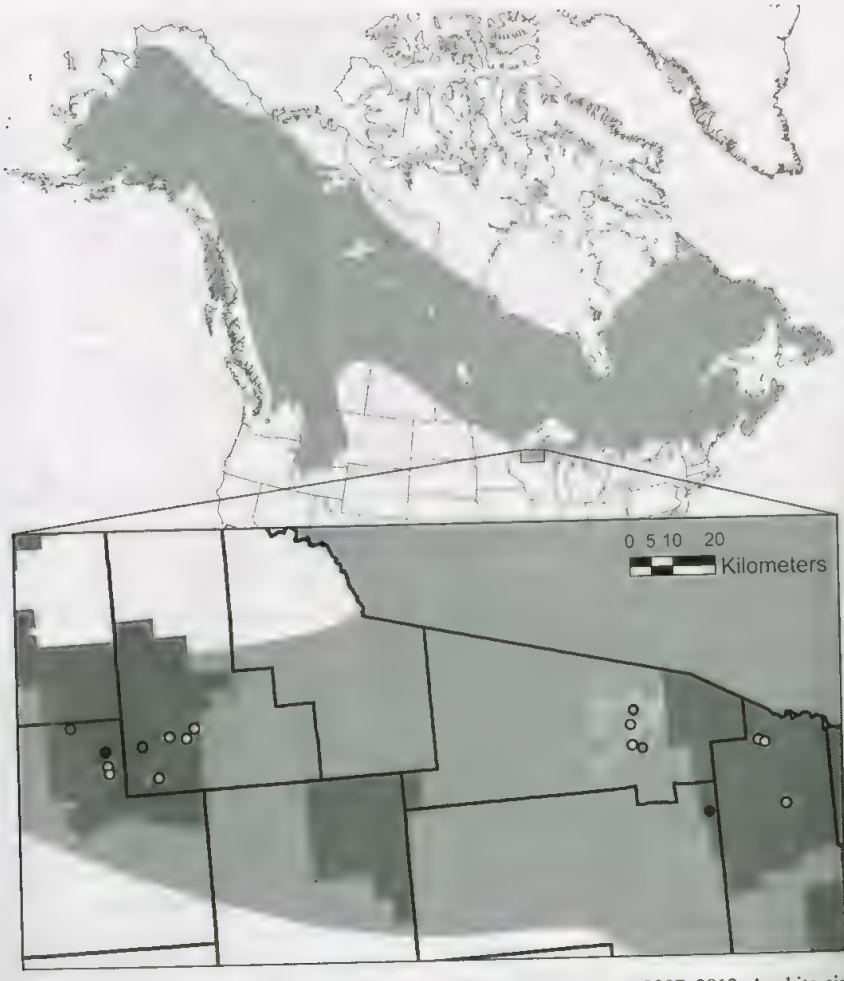

FIG. 1. Locations of 25 nests of Spruce Grouse in our study areas in Wisconsin, 2007–2012. A white circle is used to represent one nest, a gray circle represents two nests in close proximity, and a black circle represents three nests in close proximity. Medium gray represents the range of Spruce Grouse, dark gray indicates Chequamegon-Nicolet National Forest, and light gray indicates Vilas County Forest. Range is based on Scott (1943), Boag and Schroeder (1992), Dunn and Alderfer (2006), Worland et al. (2009), and eBird (2012).

the nest without approaching it. The interval between nest checks averaged 11 days (range = 3–24 days). To estimate nest initiation date and hatching date, we assumed an egg-laying rate of 1 egg every 1.4 days and 22 days of incubation (Boag and Schroeder 1992). After hatching and fledging, we visually assessed the contents of the nest and homed to the female to observe her behavior and search for young. We considered successful nests to be those that hatched at least 1 chick. On most visits the presence of young was confirmed visually, but on some visits we determined young were present because of hen behavior (Haas 1974). Hens with chicks were usually on the ground; if we approached closely, they would often call, appear agitated, and occasionally perform a distraction display, and chicks could often be heard vocalizing. Hens without young were more often in trees, and rarely vocalized. We monitored surviving broods until they dispersed from their mothers, which, based on seven young (from four broods) that we radiocollared while still with their mothers in early fall, was between mid-September and mid-October. We determined overall productivity based on number of young present on the last visit (4–23 Sept) before young dispersed in fall and estimated productivity as young/female

including all nesting attempts and three instances where hens did not nest. We also report young/successful nest.

Vegetation Measurements.—We measured vegetation at nests and paired random locations in similar habitat to determine small-scale nest-site characteristics selected by grouse, and to identify nest-site characteristics useful for predicting nest survival. We sampled habitat using a modified BBIRD protocol (Martin et al. 1997), within an 11.3-m radius plot centered at nests, and at a paired random point that was a random direction and distance (100–200 m) from nests. Random points were redrawn if they fell in forest with <50% conifer stems. This methodology allowed us to focus on relatively small-scale differences in habitat structure within suitable conifer habitat; it was clear from the literature and our own observations that Spruce Grouse do not nest in areas without conifers. We sampled vegetation from 12 August 2010 to 7 September 2010, from 1 June 2011 to 4 August 2011, and on 26 June 2012. We measured distance to lowland–upland edge using a measuring tape if the edge was within 15 m of the plot, otherwise we used aerial photos and forest reconnaissance maps in ArcMap 10 (ESRI 2010). We used a vertical densitometer to measure percent canopy cover (Stumpf 1993) using 100 readings taken every step along the circumference of the 11.3-m radius plot and then by bisecting the plot. Within four quadrants, we identified trees and shrubs to species or genus and tallied them in six classes: small saplings (<2.5 cm dbh, >1 m tall), large saplings (2.5–8 cm dbh), pole trees (>8–23 cm dbh), saw trees (>23–38 cm dbh), large saw trees (>38 cm dbh) and snags (dead, >1.4 m tall). In five 1-m^2 plots, one centered on the nest or center point, and four plots touching the center plot in the four cardinal directions, we estimated percent ground cover (<50 cm height) in several classes (moss, grasses, sedges, coniferous trees and shrubs, broadleaf trees and shrubs, pine needles, leaf litter, fallen logs, brush, bare ground, blueberry [*Vaccinium myrtilloides* or *V. angustifolium*], bog Labrador tea [*Ledum groenlandicum*], leatherleaf [*Chamaedaphne calyculata*], forbs, and ferns). We recorded the species of tree nearest to the nest or random point.

We measured vegetation density and nest concealment in three different ways. (1) At 5 m from the nest or center point in the four cardinal directions, we used a vegetation coverboard (Nudds 1977) to estimate percent cover of vegetation in four height classes (0–0.5 m, 0.5–1.0 m, 1.0–1.5 m, 1.5–2.0 m). We used these classes to generate estimates of vegetation density cover from 0–2 m, 0–1 m, 0–0.5 m, and also used the horizontal coefficient of variation (CV) of the four 0–0.5 m coverboard readings to examine whether the variability in distribution of understory density was an important factor. (2) We visually estimated overhead concealment at 1 m above the nest in 5% increments. (3) We visually estimated overall nest concealment based on an index devised by Keppie and Herzog (1978) that rated lateral concealment as 25% for next to the base of a tree and 0% for not, rated additional lateral concealment as 0, ≤25%, or >25%, and rated overhead concealment as 0, ≤25, 26–50, or >50%. We considered all nests within 0.1 m of the base of a tree to be next to a tree, and considered nests 0.1–0.3 m from the base of a tree to be next to a tree only if the lower branches concealed most of the nest from that direction. Nests >0.3 m from a tree were considered not to be next to a tree. Keppie and Herzog (1978) combined lateral and overhead concealment ratings to an overall concealment measure of 0–25 (very poor), 26–50 (poor), 51–100 (good), or >100 points (very good). For our analysis, we added together the midpoints of these value ranges for the three estimates (e.g., for 0, ≤25%, >50%, then 0 + 12.5 + 75 = 87.5), resulting in a concealment index value for each nest with 13 possible values ranging from 0 to 162.5.

Statistical Analyses.—We used information theoretic techniques to model which habitat features distinguished random sites from nest sites. We formulated 19 a priori models, based on the literature and our own observations, that we thought would be good indicators of nest sites for Spruce Grouse (Table 1). We summarize the mean and spread of our habitat variables in Appendix A. We did not allow highly correlated variables ($|r| > 0.7$) to appear in the same model, to avoid issues with multicolinearity. We used generalized linear mixed models with a binomial distribution and logit link function (SAS PROC GLIMMIX; Littell et al. 2006) and evaluated these models using Akaike's Information Criterion for small sample sizes (AIC_c, Burnham and Anderson 2002). We included hen ID and nest/paired-random ID as random effects in models to account for several hens with >1 nest and the

TABLE 1. A priori candidate models of habitat variables used to predict nest survival and to distinguish nest sites from paired random points for Spruce Grouse in northern Wisconsin.

Candidate model	Variables
Models used in both the nest survival and nest site analyses	
0–0.5 m vegetation density	Percent vegetation cover 0–0.5 m[a]
0–0.5 m vegetation density and distribution	Percent vegetation cover 0–0.5 m[a] + horizontal coefficient of variation (CV) of 4 coverboard readings
0–1 m vegetation density	Percent vegetation cover 0–1 m[a]
0–2 m vegetation density	Percent vegetation cover 0–2 m[a]
Blueberry cover	Blueberry cover[b]
Canopy cover	Canopy cover[c]
Concealment index	Concealment index value[d]
Conifer small sapling	Number of conifers <2.5 cm dbh[e]
Conifer tree and shrub	Conifer tree and shrub cover[b]
Edge	Distance to upland–lowland edge (m)
Ericaceous cover	Sum of blueberry, bog Labrador tea, leatherleaf covers[b]
Bog Labrador tea cover	Bog Labrador tea cover[b]
Low ground cover	Sum of grass, sedge, conifer tree and shrub, broadleaf tree and shrub, ericaceous, forbs, fern cover[b]
Moss cover	Moss cover[b]
Number of trees (excludes small saplings)	Number of trees ≥2.5 cm dbh[e]
Overhead cover	Estimated percent cover over nest
Percent large saplings	Percent large saplings (2.5–8 cm dbh) of trees ≥2.5 cm dbh[e]
Quality conifer	Number of black spruce, upland spruce, tamarack, jack pine[e]
Models only used in the nest survival analysis	
Julian day	Julian day of the nest check
Julian day + Julian day^2	Julian day of the nest check and Julian day squared
Year	Year of the nest
Model only used in the nest site analysis[f]	
Percent broadleaf	Percent broadleaf trees (excludes small saplings)[e]

[a] Measured with a coverboard (Nudds 1977)
[b] Measured at five 1-m^2 plots, one centered at nest, others abutting central plot in four cardinal directions.
[c] Number of points/100 with closed canopy, measured using a vertical densitometer (Stumpf 1993).
[d] Estimate of lateral and overhead nest concealment (based on Keppie and Herzog 1978).
[e] Counted within a 11.3-m radius circle centered on the nest
[f] We removed this model from the nest survival analysis as it failed to converge (only five nests had any broadleaf cover).

possible non-independence of a nest and its paired random point. We used a likelihood ratio test between the best model and intercept-only model to confirm model fit ($\chi^2 = 16.26$, $P < 0.0001$).

To relate habitat features to nest survival, we used the logistic exposure method (SAS PROC GENMOD, Shaffer 2004) and evaluated 21 a priori models (Table 1) using AIC_c (Burnham and Anderson 2002). The logistic-exposure model estimates daily survival rate (DSR), rather than using binary nest success or failure, to relate to explanatory variables. We initially used a random effect in models to account for several nests from the same hens; however, this variable was found to be unimportant, so our final analysis included no random effect. We used a likelihood ratio test between the best model and intercept-only model to confirm model fit ($\chi^2 = 8.62$, $P = 0.013$).

We also estimated adult and juvenile survival using logistic exposure (SAS PROC GENMOD. Shaffer 2004) to examine survival over the intervals between telemetry points. For juvenile survival, we used telemetry points for the seven birds we caught and radiomarked in fall while still with their mothers, and we also included observations of 54 chicks observed with radiomarked hens. We used two different ways to estimate juvenile survival because of uncertainty about biases: (1) we included an interval between an estimated hatch date and the first brood check and assumed all eggs that did not remain in the nest hatched, and any young we did not observe had died before the first brood check, (2) we ignored the interval between hatching and the first brood check, and modeled survival of only the young seen with the hen. The first method is a potential underestimate of survival, if clutches experienced

partial predation or if we failed to detect young when they were small. The second method is a potential overestimate of survival, because it ignores initial chick mortality.

To estimate adult survival, we used intervals between telemetry points on 51 radiocollared birds. We did not age birds; however, the majority of birds we designated as adults (45) were captured between 31 March and 16 May, making them at least 9 months of age at initial capture. For juvenile survival, we examined if effects of year, Julian day, Julian day + Julian day^2, study site (western sites vs. eastern sites), or days since hatching (for nests we could approximate a hatch date within ±6 days) improved models. We found that the best model for both of our methods of estimating juvenile survival included days since hatching, and we used that term in both juvenile models. For adult survival (males and females combined), we examined the above variables as well as sex. No variables improved the adult survival models, so we modeled overall adult survival using the null (constant survival) model. We also calculated estimates for adult male survival, using the best model, Julian date, and adult female survival using the null model (a model for adult female survival including a year effect had a lower AIC_c value, but we were unable to obtain a reliable estimate from this model because of convergence problems). We transformed the daily survival rate generated through logistic exposure to an annual survival rate (ASR) using $ASR = DSR^{365.25}$. We multiplied by 100 when reporting ASR to express as a percentage of birds surviving one year. We determined whether our population was a source or sink by calculating the rate of increase of the population, λ, using

$$\lambda = \text{annual adult female survival} + (\text{annual juvenile female survival} \times \text{annual number of famale offspring/female})$$

where $\lambda > 1$ for a growing population and <1 for a declining population (Pulliam 1988, Podolsky et al. 2007). Because we could not determine the sex of young birds, we assumed juvenile female survival was the same as our general juvenile survival estimate. Assuming a 50:50 sex ratio, we divided the number of offspring by 2 to represent the number of female offspring. When using the first method of determining juvenile survival (from hatch date), we assumed the number of offspring was equal to the hatched eggs and calculated the survival of those individuals; however when using the second method of determining juvenile survival (from the first brood check), we assumed the number of offspring was equal to the number of chicks we observed and calculated survival of the number of chicks we observed.

RESULTS

We radiocollared 30 female Spruce Grouse from 2007–2012. Nine hens were killed by unknown predators before they were able to nest, one hen dispersed so far that we lost its signal, and two hens apparently did not nest, including one that did not nest in two consecutive years. Both non-nesting hens were in the same swamp, where in 2011, nesting may have been precluded by an intolerably high density of deerflies (*Chrysops* spp.). We found 25 nests, 24 of which were from 18 radiocollared hens, and one from an uncollared hen which we located incidentally (Fig. 1). We obtained successive nest locations in consecutive years for four of the radiocollared hens and two hens re-nested following failure. Mean estimated nest initiation date was 17 May (range = 4 May–6 Jun, SE = 2.5, n = 17) and mean estimated hatch date was 16 Jun (range = 1 Jun–1 Jul, SE = 2.2, n = 15). Mean clutch size was 6.3 (range = 3–8, SE = 0.3, n = 24), with clutches from 3–5 eggs representing likely re-nests and clutches of 5–8 eggs initial nests.

Concealment index was clearly the best predictor of nest sites, with an AIC_c weight of 0.98 (Table 2). As expected, increased concealment was associated with nest sites of Spruce Grouse (Fig. 2). All nests were on the ground ≤0.7 m from the base of a tree. Although radiotelemetry locations showed that eight of 18 hens used jack pine stands (mean = 38% of points in jack pine, range = 9–72%), we found only one nest in jack pine upland, next to the base of a jack pine snag with a broken trunk that provided a roof to the nest. Two nests were on upland edges, 5 and 21 m away from black spruce–tamarack swamps: one beneath a balsam fir, and the other beneath a jack pine in an area dominated by spruce. Twenty-two nests (88%) were in black spruce–tamarack lowland: 18 beneath a black spruce, 3 beneath a tamarack, and 1 beneath a black spruce snag. The trees nearest to the plot center at 24 random points included 12 black spruce, 4 balsam fir, 3 tamarack, 2 jack pine, 1 red pine, 1 quaking

TABLE 2. Results of generalized linear mixed models with binomial distributions and logit link functions showing habitat differences in northern Wisconsin between Spruce Grouse nest locations (n = 24) and paired random points. Plus or minus indicates the direction of the relationship. Models with the lowest ΔAIC_c and highest weight (w_i) are the best-supported models. Only models better than the intercept-only model are shown (weights are based on the full model set in Table 1).

Model	K[a]	ΔAIC_c	w_i
Concealment index (+)	4	0.00[b]	0.98
Overhead cover estimate (+)	4	9.13	0.01
0–0.5 m vegetation density (+)	4	12.33	<0.01
Moss cover (+)	4	12.39	<0.01
Canopy cover (−)	4	12.75	<0.01
0–1 m vegetation density (+)	4	13.27	<0.01
Conifer tree and shrub cover (+)	4	13.62	<0.01
Bog Labrador tea cover (+)	4	13.84	<0.01
Intercept-only	3	14.08	<0.01

[a] Number of parameters.
[b] AIC_c of best model = 54.55.

aspen (*Populus tremuloides*), and 1 upland (black or white) spruce. Spruce Grouse showed a preference for black spruce as a nest concealment tree (χ^2 = 5.04, P = 0.025, df = 1).

Seventeen of 25 nests were successful. One nest failure was caused by abandonment, likely related to our attempt to set up a camera at this nest (we excluded this nest from the nest survival analysis). We attribute the other seven nest failures to unknown predators. In two of those instances the females were killed, and in two other instances the female escaped but lost feathers. Nests fledged an average minimum of 3.2 young (range = 1–6, SE = 0.4, n = 15), though our estimates of initial brood size are likely low because of thick vegetation at brood locations and because we did not want to stress young broods through extended observation. The mean number of young that survived until fall was 1.0/hen (range = 0–5, SE = 0.4, n = 21), including all nests (and 3 instances of non-nesting) and 1.9/hen, including only successful nests (range = 0–5, SE = 0.5, n = 11).

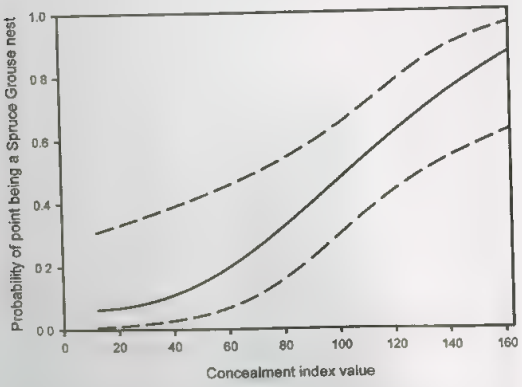

FIG. 2. Result from a generalized linear mixed model with a binomial distribution and logit link function showing the relationship between nest concealment index values (larger numbers indicate more concealment; based on Keppie and Herzog 1978) and the probability that a point is a nesting location of Spruce Grouse. Dashed lines are 95% confidence limits. We compared 24 nesting locations of Spruce Grouse to 24 paired randomly selected points in northern Wisconsin.

The overall daily survival rate of nests was 0.985 (95% CI = 0.969, 0.993). The best model predicting nest survival showed inverse relationships with 0–0.5 m vegetation density (β = −6.33, 95% CI = −11.25, −1.42) and horizontal CV vegetation density (β = −0.09, 95% CI = −0.16, −0.01) and had an AIC_c weight of 0.31 (Table 3), though there appeared to be a threshold effect where only plots with the highest densities and greatest values of horizontal heterogeneity of 0–0.5 m vegetation tended to have unsuccessful nests (Fig. 3). There was some support for models showing inverse relationships with moss cover (β = −0.1, 95% CI = −0.22, 0.02), ericaceous cover (β = −0.04, 95% CI = −0.07, −0.0006), and bog Labrador tea cover (β = −0.03, 95% CI = −0.07, 0), which had AIC weights from 0.20–0.08 (Table 3).

Our estimated DSR of adults (n = 51 birds) was 0.998 (95% CI = 0.997, 0.999), yielding an ASR of 45% (95% CI = 32%, 58%). Adult male survival (n = 28, DSR = 0.998, 95% CI = 0.997, 0.999; ASR = 54%, 95% CI = 33%, 71%) was higher than female survival (n = 23, DSR = 0.998, 95% CI = 0.996, 0.999; ASR = 40%, 95% CI = 21%, 59%). Our juvenile DSR based on

TABLE 3. Results of logistic exposure models predicting daily survival rate of nests of Spruce Grouse in northern Wisconsin, 2007–2012. Models with the lowest ΔAIC_c and highest weight (w_i) are the best-supported models. Only models better than the intercept-only model are shown (weights are based on the full model set in Table 1).

Model	K[a]	ΔAIC_c	w_i
0–0.5 m vegetation density and distribution	3	0.00[b]	0.31
Moss cover	2	0.87	0.20
Ericaceous cover	2	2.37	0.09
Bog Labrador tea cover	2	2.77	0.08
Intercept only	1	4.17	0.04

[a] Number of parameters.
[b] AIC_c of best model = 34.94

number of eggs presumed to hatch (n = 88) was 0.995 (95% CI = 0.991, 0.997; ASR = 14%, 95% CI = 4%, 32%). Our juvenile DSR based on number of young seen (n = 54) was 0.996 (95% CI = 0.993, 0.998; ASR = 24%, 95% CI = 8%, 45%). Based on these estimates, recruitment (mean number of female offspring/female/year × juvenile survival) based on number of eggs presumed to hatch was 0.27 (95% CI = 0.07, 0.59) and based on number of young seen was 0.25 (95% CI = 0.09, 0.46). Estimates of λ were 0.67 (95% CI = 0.27, 1.18) using number of eggs presumed to hatch, and 0.65 (95% CI = 0.29, 1.04) based on number of young seen.

DISCUSSION

Black spruce swamp was the most common nesting habitat for Spruce Grouse in Wisconsin, similar to northern Minnesota (Haas 1974) and Alaska (Ellison 1971), but unlike Spruce Grouse in Michigan or Ontario where jack pine has been reported more commonly (Robinson 1980, Naylor

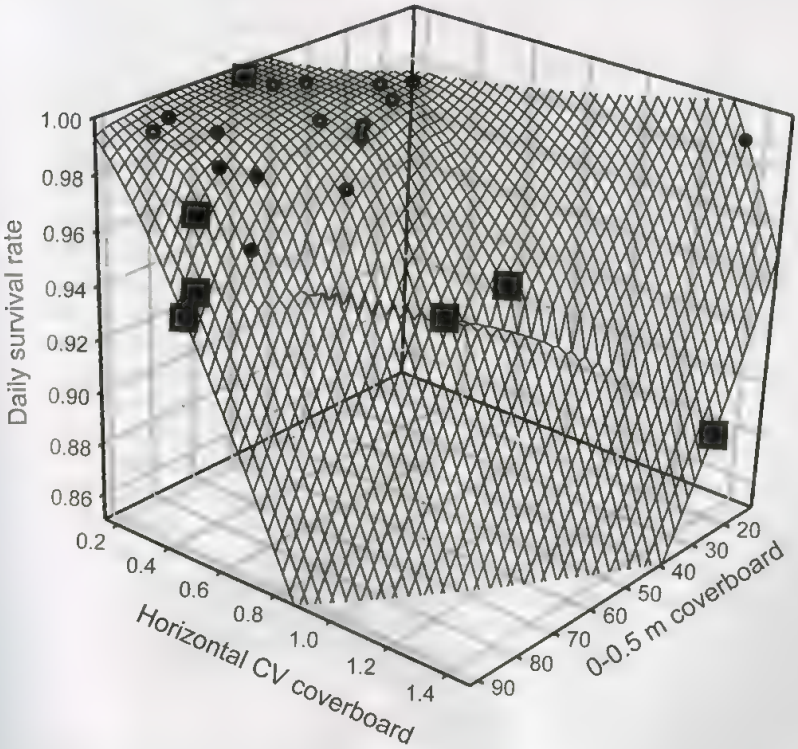

FIG. 3. Daily survival rate of nests of Spruce Grouse in Wisconsin, 2007–2012, as predicted by percent vegetation cover measured with a 0–0.5 m coverboard and horizontal coefficient of variation (CV) of those coverboard readings. Successful nests are represented by black circles, larger black squares indicate nest failure.

et al. 1988, D'Eon 1997), or sites in Alberta where the grouse typically use lodgepole pine and white spruce (McCourt et al. 1973, Keppie and Herzog 1978). The relative scarcity of jack pine at our study areas, especially on CNNF, is not the sole reason for the use of black spruce swamps for nest sites; jack pine was used often by flocks in winter and as display sites for males (Anich et al. in press), and even hens that used jack pine at other times of year selected nest sites in black spruce lowlands. Perhaps the selection for lowland areas here at the southern edge of Spruce Grouse range is related to providing a suitably cool and moist microclimate for the eggs, given that eggs from Spruce Grouse are known to dry faster than eggs from Ruffed Grouse (*Bonasa umbellus*; Bendell and Bendell-Young 2006). Another possibility is that Spruce Grouse have evolved a preference for conifer swamps because, except in winter, these sites are poor habitat for mammalian predators. Mammalian mesopredators such as raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), fisher (*Martes pennanti*), and red fox (*Vulpes vulpes*) may avoid large conifer swamps because of a limited prey base and the energy required to travel through standing water, thick vegetation, and uneven, hummocky terrain (Berg 1992).

No single habitat variable we measured was as effective at explaining nest locations as the nest concealment index developed by Keppie and Herzog (1978). We were somewhat surprised that such a coarse estimate performed so well; however, numerous studies of grouse have found concealment to be an important feature of nest locations (Schieck and Hannon 1993, Gregg et al. 1994, Campbell et al. 2002), presumably by providing visual, and perhaps olfactory, barriers to detection by predators (Bergerud and Gratson 1988). Increased concealment at nests has also been found in other avian taxa (Sutherland and Maher 1987, Holway 1991).

However, the concealment index did not rank among the best models in predicting nest survival. Redmond et al. (1982) also found no relationship between concealment and nest success in eastern *canace* Spruce Grouse, for which concealment was often high, but did find that greater concealment was related to nest success in the western *franklinii* subspecies, for which concealment was generally low. D'Eon (1997) also found no relationship between concealment and nest success in Spruce Grouse and suggested concealment is more important at sites that are relatively open with patchy cover compared to sites that have dense and uniform cover throughout. Many studies have found that greater concealment at nests sites did not translate to greater nest success (Sutherland and Maher 1987, Colwell 1992, Campbell et al. 2002). Presumably, for many species, concealment can help provide protection from predators, but it is likely there are other, perhaps predator-specific (e.g., Benson et al. 2010b) or habitat-specific factors at work that may be more important predictors of predation, especially at sites where many nests are fairly well concealed.

Although concealment index values were not good predictors of nest survival, the best model predicting nest survival, 0–0.5 m vegetation density and distribution, does describe concealment at nest sites, and indicated that fairly dense and uniform cover was associated with good nest survival (Fig. 3). Nests without uniform vegetation cover had poorer survival, as three of four nests with CV horizontal vegetation readings over 0.7 failed (Fig. 3). We were surprised that there was an overall inverse relationship between 0–0.5 m vegetation density and nest survival, and the three nests with the densest vegetation failed (Fig. 3). Redmond et al. (1982) suggested predators of Spruce Grouse may preferentially target especially dense vegetation clumps, which could give moderately dense nest sites greater suitability than extremely dense nest sites (see also Benson et al. 2010a). Other studies have found a preference for intermediate levels of concealment. For example, Götmark et al. (1995) argued that there was a trade-off between nest concealment and a view of the nearby surroundings, evidenced by selection of intermediate concealment for nests of Song Thrushes (*Turdus philomelos*). Wiebe and Martin (1998) demonstrated that a potential cost of extremely dense nest cover for White-tailed Ptarmigan (*Lagopus leucura*) was greater difficulty escaping from predators. This finding is supported by our results: the female with the highest 0–0.5 m vegetation density was killed by a predator during incubation, while the female with the third-densest nest barely escaped predation on the nest, losing feathers. The following year, the 0–0.5 m vegetation density at that female's nest measured 60%, down from 86%. The cryptic plumage of Spruce Grouse may make nest sites with intermediate vegetative concealment tenable, compared to nesting opportunities for bird species that are less cryptic.

There was some support for an inverse relationship with moss cover and nest survival. Presumably, sites at which we estimated greater moss cover had less cover of conifer shrubs. Models of bog Labrador tea and ericaceous vegetation cover were also better than the null model, but these inverse relationships were in the opposite direction from what we hypothesized, and were fairly weak. Perhaps ericaceous vegetation is not as effective at concealing birds as cover of short conifers, making sites with greater ericaceous vegetation less well concealed compared to sites with short conifers but less overall ericaceous cover. Or perhaps long-stemmed ericaceous plants do not effectively conceal the nest from certain groups of predators (e.g., small mammals, weasels).

Our apparent nest success estimate (17/25, 68%) was higher than the 29% (19/66) from Alberta (Keppie 1982), 33% (4/12) from Minnesota (Haas 1974), and 51% (33/65) from Ontario (D'Eon 1997), but lower than 76% (16/21) from Alaska (Ellison 1974), 81% (30/37) from New Brunswick (Keppie 1982), 83% (5/6) in Minnesota (Pietz and Tester 1982), 88% (14/16) in Maine (Whitcomb et al. 1996), and 89% (8/9) from Michigan (Robinson 1980). However, nest success is only one component of overall productivity, and our chick survival through the brood period was somewhat low. Whitcomb et al. (1996) estimated productivity of 0.6 young/female in Maine, and suggested that productivity tends to be poorer on the southern edge of the range. Our productivity estimate of 1.0 young/female was higher than Whitcomb et al. (1996), similar to estimates of 0.8 and 1.1 from Alberta (Keppie 1982, Smyth and Boag 1984), and lower compared to 1.9 in Washington (Zwickel and Brigham 1970), 2.0 in New Brunswick (Keppie 1982), 4.1 in Ontario (Lumsden and Weeden 1963) and 5.4 in Alaska (Ellison 1974). However, direct comparison among these studies is difficult, as biases likely vary among the different methods that were used: radiotracking, use of pointing dogs to find birds, and the ratio of juveniles to females in birds shot by hunters. We were not able to calculate productivity estimates of young/female (including all nest attempts) based on information from Michigan or Minnesota, but estimates of young per successful nest averaged 2.6 (based on brood size in Aug) for Minnesota (n = 13, Haas 1974) and 3.7 (based on brood size in late Jul–Aug) for Michigan (n = 48, Robinson 1980). These estimates are slightly higher than our September estimate of 1.9 young/successful nest, but are based on visual sightings of unradioed hens slightly earlier in the year which may be biased towards detecting larger broods. We found no differences between vegetation at brood locations selected by hens compared to random points, indicating hens are using habitat similar to what is available (Anich et al. in press). This may indicate brood habitat is not limiting at our sites, or may indicate vegetative factors are not driving brood habitat quality. Clearly, more information on causes and factors affecting brood survival is needed.

Our mean estimates of annual juvenile recruitment using our two methods of estimating juvenile survival were very similar, suggesting our estimates were robust. However, a number of factors, particularly limited information on age classes, difficulty observing young chicks, and a somewhat small sample size of juveniles, add some uncertainty to our results. Despite these caveats, we used estimates we derived from our own data; many investigations simply use estimates from the literature for one or more model parameters. Our mean values for λ indicate that this population may be declining, but the upper confidence limit exceeds one, leaving open the possibility of a stable or slightly growing population.

Although a number of investigators have estimated survival of Spruce Grouse, it is difficult to compare directly our estimates to others that used a variety of methods over differing time periods. In Alaska, based on surveys with dogs across a study area over 3 consecutive years, Ellison (1974) estimated 20 and 25% survival of juvenile males over a 9-month period, and 21 and 26% survival of juvenile females over an 11-month period. Although emigration and immigration, among other assumptions, could significantly affect Ellison's estimates, they were in the range of our juvenile survival estimate. Beaudette and Keppie (1992) estimated juvenile survival for a 54-day period prior to autumn dispersal as 72%; for the subsequent period, disperser survival was 73% over 65 days and non-disperser survival was 83% over 52 days, but they did not estimate survival annually, or between hatching and autumn. Our estimates of adult survival were similar to many in the literature. In Michigan, based on encounters with banded birds, Robinson (1980) estimated annual survival in adults over 1 year old as 50% for males and 45% for females. In New Brunswick, Keppie (1987) used dogs to locate color-marked Spruce Grouse and reported

annual survival of 44% for adult males, 53% for adult females, 44% for yearling males, and 46% for yearling females. Ellison's (1974) estimates of annual survival for adult males were 26 and 37% for 2 different years, and estimates for adult females were 36 and 50%. In Alberta, Keppie (1979) reported fairly high annual survival rates, ranging from 74–82% for adult males, 64–71% for adult females, 71–80% for yearling males, and 31–65% for yearling females.

Nest predators at our sites are unknown, as failed nests or kill sites often had little sign to interpret, but we assume canids, hawks and owls, mustelids, and small mammals are likely predators (Robinson 1980, Boag and Schroeder 1992). Learning more about specific predators could improve our understanding of which factors are important to breeding success (Benson et al. 2010b). It is generally assumed that lateral cover is of greater value to protection from mammalian predators, while overhead cover protects from avian predators (Wiebe and Martin 1998). The fact that the model that best predicted daily nest survival had no overhead cover component points to a greater influence of mammalian predators at our sites.

This study demonstrates that Spruce Grouse nesting in our area are strongly tied to black spruce swamps. Actions that increase heterogeneity of low vegetative cover in these swamps, such as strip-cutting of black spruce, could negatively affect nesting success. Preserving black spruce swamps is critical to ensuring the persistence of populations of Spruce Grouse in Wisconsin. Protecting these swamps is also important for preserving local avian biodiversity, particularly on the southern edge of boreal forest, where boreal species are limited to such habitats (Hoffman and Mossman 1993, Calmé et al. 2002). However, preserving these conifer swamps and the birds that inhabit them may be an ever-increasing challenge in the face of climate change.

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APPENDIX A. Mean, 95% confidence interval, and range of habitat data recorded at 24 nests of Spruce Grouse and paired random points in Wisconsin, 2007–2012.

	Mean	95% CI	Range
0–0.5 m vegetation density[a]	58.3	52.0, 64.5	5.0–97.3
0–0.5 m vegetation distribution[b]	0.6	0.5, 0.7	0.1–1.5
0–1 m vegetation density[a]	50.5	45.2, 55.7	6.3–80.3
0–2 m vegetation density[a]	43.9	39.1, 48.7	7.8–77.8
Blueberry cover[c]	6.6	4.3, 8.9	0.0–30.0
Bog Labrador tea cover[c]	19.4	14.0, 24.8	0.0–65.0
Canopy cover[d]	47.5	40.8, 54.1	9–89
Concealment index[e]	101.6	87.8, 115.4	12.5–162.5
Conifer small sapling[f]	78.1	62.9, 93.4	1–215
Conifer tree and shrub[c]	17.7	13.2, 22.1	0.0–58.0
Edge	91.9	68.2, 115.7	5–383
Ericaceous cover[c]	36.9	29.5, 44.4	0.2–85.0
Low ground cover[c]	85.6	75.6, 95.6	21.4–160.0
Moss cover[c]	68.2	59.6, 76.8	0.4–95.4
Number of trees (excludes small saplings)[f]	102.2	90.6, 113.7	41–205
Overhead cover	42.0	33.4, 50.7	0–95
Percent broadleaf[f]	4.9	1.0, 8.8	0.0–64.8
Percent large saplings[f]	68.3	62.5, 74.1	19.5–97.8
Quality conifer[f]	157.0	130.8, 183.2	5–333

[a] Measured with a coverboard (Nudds 1977).
[b] The horizontal coefficient of variation of 0–0.5 m coverboard (Nudds 1977) readings in four cardinal directions.
[c] Measured at 5.1 m^2 plots, one centered at nest, others abutting central plot in four cardinal directions.
[d] Number of points/100 with closed canopy, measured using a vertical densitometer (Stumpf 1993).
[e] Estimate of lateral and overhead nest concealment (based on Keppie and Herzog 1978).
[f] Counted within a 11.3-m radius circle centered on the nest.

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KELP GEESE (*CHLOEPHAGA HYBRIDA*) AND FLIGHTLESS STEAMER-DUCKS (*TACHYERES PTENERES*) IN THE BEAGLE CHANNEL: THE IMPORTANCE OF ISLANDS IN PROVIDING NESTING HABITAT

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ABSTRACT.—We describe the nest-site characteristics and breeding habitat use of Kelp Geese (*Chloephaga hybrida*) and Flightless Steamer-Ducks (*Tachyeres pteneres*) along 137 km of coastline on the northern shore of the Beagle Channel, Argentina, and 87 km of island coastline. We examined the importance of vegetation cover, predation, and tourism on the distribution of nests among islands. We found all nests only on islands and islets. Nesting sites for both species were strongly associated with higher proportions of high vegetation cover (shrubs). Kelp Geese were also associated with the absence of terrestrial predators. Tourist presence on islands was not associated with the occurrence of nests for either species. The northern coasts of the Beagle Channel and the islands and islets along the channel have similar habitat types. However, the islands and islets are relatively inaccessible to mammalian terrestrial predators compared to the coast of the channel where terrestrial predators are frequently recorded. Therefore, islands and islets seem to provide a relatively safe nesting habitat for Kelp Geese and Flightless Steamer-Ducks by offering refuge mainly from ground predators. Additionally, habitat changes caused by increased human disturbance along the northern shore of the Beagle Channel may also explain the presence of nests only on islands and islets, though further studies are needed to assess these effects. This study contributes new information on the breeding habitat and nesting sites of Flightless Steamer-Ducks and Kelp Geese in the Beagle Channel, to assist in the identification of priority breeding sites and habitats to protect. Also, it highlights the importance of islands and islets of the Beagle Channel as safe breeding refuge for these two ground nesting seabirds.
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Key words: Beagle Channel, Flightless Steamer-Duck, islands, Kelp Goose, nesting habitat.

Birds select their breeding habitat based on factors that determine its quality, such as food resources, presence of predators, and microclimate (Bried and Jouventin 2002). For most species, breeding habitat must be located close to abundant food resources, provide adequate nesting substrate, and offer protection against predators (Furness and Monaghan 1987, García Borboroglu and Yorio 2004, Yasué 2006). From a conservation perspective, the determination of nesting habitat characteristics can be used to identify environments and habitat features to protect. This information is also critical for developing conservation strategies and effective management plans.

Most seabirds nest in relatively inaccessible sites in order to avoid or minimize the risk of ground predators and human disturbance (Partridge 1978, Buckley and Buckley 1980, García Borboroglu and Yorio 2007, Agüero et al. 2010). Additionally, many species nest in areas with greater vegetation cover which offers the advantage of increased concealment against predators and other benefits (Clark and Nudds 1991, Butler and Rotella 1998, Opermanis et al. 2001). Mammalian terrestrial predators represent an important threat for ground nesting coastal birds along the Beagle Channel, Tierra del Fuego. The introduced American mink (*Neovison vison*) and South American grey fox (*Pseudalopex griseus*), together with the native southern river otter or huillín (*Lontra provocax*), and the Fuegian culpeo fox (*Pseudalopex culpaeus lycoides*) are predators that have been recorded along the coast of the Beagle Channel (Atalah et al. 1980, Massoia and Chébez 1993, Lizarralde and Escobar 2000, Gomez et al. 2010, Valenzuela et al. 2013a). A recent study on the impact of the American mink on ground nesting seabirds on Navarino Island (south of the Beagle Channel) found that those species nesting solitarily, in coastal habitat with rocky outcrop shorelines and concealed nests, such as Kelp Geese (*Chloephaga hybrida*) and Flightless Steamer-Ducks (*Tachyeres pteneres*), were the most vulnerable to mink predation (Schüttler et al. 2009). On the Isla Grande de Tierra del Fuego (IGTF), along the

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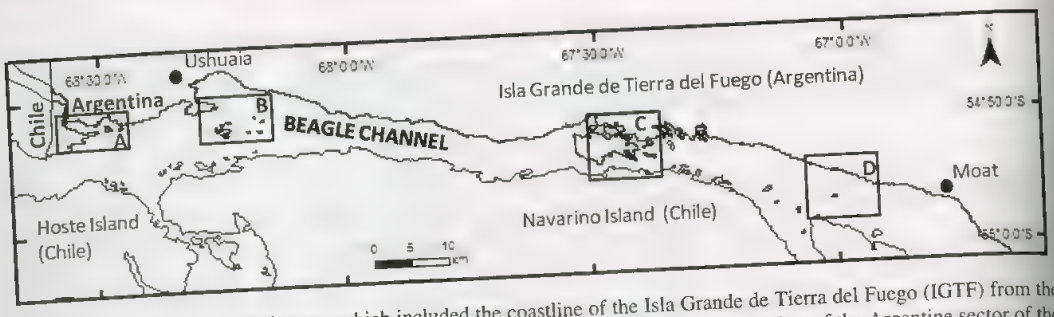

FIG. 1. Map showing study area, which included the coastline of the Isla Grande de Tierra del Fuego (IGTF) from the border with Chile in the west to Estancia Moat in the east, and 36 of the 45 islands and islets of the Argentine sector of the Beagle Channel.

northern coast of the Beagle Channel, Gomez et al. (2010) reported sea birds being a secondary prey in the mink's diet, though Valenzuela et al. (2013b) showed that in sympatry with the huillín, mink depend more on terrestrial prey.

The Argentinean coast of the Beagle Channel is currently subject to increasing human activity, including urban expansion, tourism, recreational activities and livestock grazing. The excursion to islands along the channel, mainly to observe breeding seabird colonies, is one of the main tourist attractions for people visiting Tierra del Fuego. Though the number of tour boats has increased markedly over the past years, their effect on nesting seabirds is poorly known, with the exception of a few studies on cormorants (Rosciano et al. 2013). Boats can approach the seabird colonies up to 10 m, and on a few islands, tourists are allowed to land (Schiavini and Yorio 1995). However, some islands and islets remain outside the regular tourist circuits.

The Kelp Geese and the Flightless Steamer-Ducks are strictly coastal species distributed from south-central Chile to Tierra del Fuego (Carboneras 1992). They nest solitarily and are frequently encountered along the Beagle Channel. Previous studies of these species in the channel provide qualitative records, recording species along the coast and describing their foraging and reproductive behavior (Humphrey et al. 1970, Weller 1975, Clark 1984), and most recently Raya Rey and Schiavini (2002) focused on their distribution and density along the channel. However, there is little information on the habitat requirements of these species during the breeding season. In this study, we describe nest site characteristics and the nesting habitat of Kelp Geese and Flightless Steamer-Ducks breeding along the Beagle Channel. Also, we examine the importance of vegetation cover, predation, and tourism on the distribution of nests among islands. We hypothesized that the presence of nests would be associated with islands with higher vegetation cover and absence of predators and tourists.

METHODS

Study Area.—The Beagle Channel is located at the southern tip of South America (54° S), within the Fuegian Archipelago, and extends in an east-west direction along the southern coast of the Isla IGTF, the largest island in the archipelago. Our study area included the Argentine coastline of the channel which extends along the IGTF for 220 km from the international border with Chile in the west to Estancia Moat in the east, and 36 of the 45 islands and islets of the Argentine sector of the channel (Fig. 1). The Argentine coastline of the Beagle Channel shows a rugged rocky shoreline with pocket gravel beaches that develop in the embayments (Bujalesky 2007). The typical habitats along the southern coast of the IGTF include: a) deciduous forests dominated by *Nothofagus pumilio* and *N. antarctica*, b) evergreen forests of *N. betuloides* and *Drimys winteri*, c) scrublands dominated by *Chilliotrichum diffusum* and *Berberis buxifolia*, d) grasslands, and e) peatlands and bogs dominated by *Sphagnum* spp. (Moore 1983). Habitats on the islands and islets of the Beagle Channel are similar: most islands have grasslands and scrublands dominated by *C. diffusum* and *B. buxifolia*, some of the islets are bare rock with no vegetation, and a few islands also have patches of evergreen forests of *N. betuloides* and *D. winteri* (Schiavini and Raya Rey 2001).

Nest surveys were conducted during the breeding season from November 2011–January 2012. Along the coast of the IGTF, we walked 1-km transects randomly selected in a strip 20–50 m inland, and parallel to the shore covering 137 km of the 220 km of coastline. We also

surveyed 36 islands and islets in the Beagle Channel covering the whole area of each island (87 km of island coastline, total area 231 ha). At each nesting site, we estimated average vegetation height and percentage of vegetation cover (tree, shrub, grass, or bare ground) within a 1-m radius around the nest. We also measured the distance to the nearest high-tide line, altitude above sea level, and slope of the substrate using a clinometer (Suunto type Tandem 360PC/360R).

The effect of three explanatory variables (vegetation cover, predator presence, and touristic activity) on the presence of nests for each species was assessed by generalized linear models (GLM). Because all nests were found exclusively on islands or islets (see Results), we studied island use in detail. Based on the habitat characteristics of nesting sites (see Results), we determined that the type of vegetation cover seemed to have the greatest ecological relevance for both species and used this habitat variable in the analysis. We analyzed habitat information from the 36 islands and islets surveyed. Using satellite images and field recognition, we assigned islands to one of two broad vegetation cover categories based on the dominant vegetation type: high vegetation or low vegetation cover. The "high vegetation" category included islands that had more than 40% of shrub vegetation, and the "low vegetation" category included islands with a higher percentage of grasses (which offer less nest concealment compared to shrubs) or of bare ground. Predator presence on islands and islets of the channel was assessed by means of the presence of signs (scats, tracks, sightings). Islands where signs of terrestrial predators were found were considered as "predators-present" islands, otherwise they were considered as "predators-absent." Tourist activity was assessed assigning tourism as "present" in islands that are within the itinerary of tourist vessels and are either approached by these vessels or where tourists are allowed to land.

Statistical Analyses.—Two GLM analyses were conducted: the first used the presence of nests of Kelp Geese as the response variable, and the second used the presence of nests of Flightless Steamer-Ducks. We used a binomial family distribution and a logit link function (Crawley 2007). Both analyses included the following fixed effects: vegetation cover (low/high), predators (presence/absence of terrestrial predators), and tourism (presence/absence). Our candidate model set consisted of all additive combinations of our three explanatory variables and a null model resulting in eight candidate models. We used an information-theoretic approach to guide model selection. For each model in the candidate set, we calculated Akaike's Information Criteria corrected for small sample size (AIC_c) and Akaike weights (w_i) and used ΔAIC_c and w_i to infer model support. Models with lower AIC_c values have more support from the data (Burnham et al. 2011). Based on the entire model set, we calculated model-averaged parameter estimates, unconditional standard errors and 95% CI for each explanatory variable. To determine the relative importance of each explanatory variable within a candidate model set, we summed w_i for all candidate models containing the explanatory variable under consideration, producing parameter-likelihood values scaled from zero (not-supported) to one (well-supported). Statistical analyses were performed using R software (MASS, MuMIn and lme4 packages), version 2.13.2 (R Core Development Team 2009). All values indicated are mean ± standard error (SE), unless otherwise noted.

RESULTS

We found a total of 37 nests of Kelp Geese and 18 nests of Flightless Steamer-Ducks, all on islands and islets off the coast of the IGTF (Fig. 2). Average habitat attributes of nesting sites for each species are listed in Table 1. For both species, over 50% of the vegetation cover within a 1-m distance from the nest consisted of shrubs. Kelp Geese also nested within a high percentage of grass cover. Nests of Kelp Geese were generally found closer to the high-tide line and at a lower altitude than nests of Flightless Steamer-Ducks, but these differences were not significant (Wilcoxon rank sum test, both $P > 0.05$; Table 1). Slope of the substrate on which nests were built was similar for both species (Wilcoxon rank sum test, $P = 0.69$).

The best-supported model for describing variation in the presence of nests of Kelp Geese on islands contained the explanatory variables vegetation cover and predators (Table 2). The model containing vegetation cover, predators, and tourism also received substantial support. However, only vegetation cover and predators had large parameter likelihood values and 95% CI that did not include zero, indicating their importance for explaining variation in the presence of Kelp Geese nests (Table 3). Nests of Kelp Geese were present on islands with high vegetation cover and absence of predators. Tourist presence on islands offered

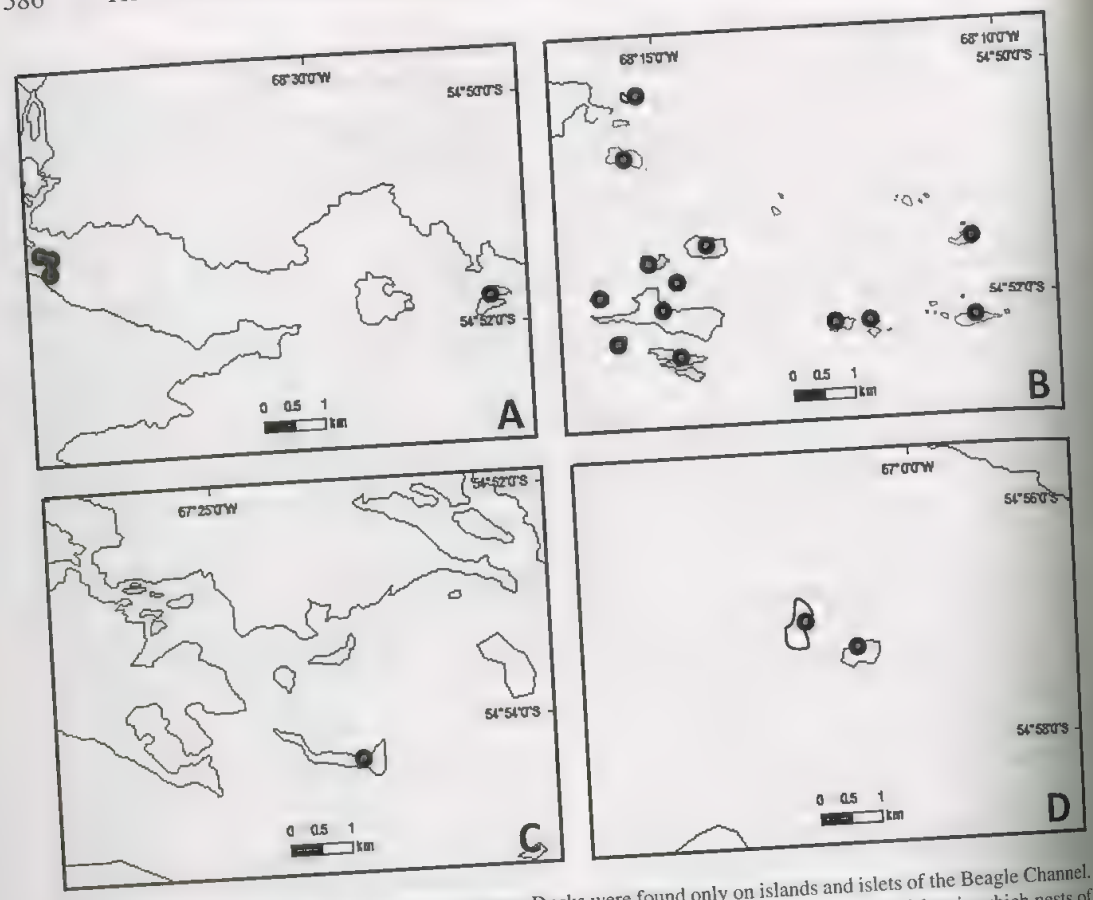

FIG. 2. Nests of Kelp Geese and Flightless Steamer-Ducks were found only on islands and islets of the Beagle Channel. A-D show in detail sectors of our study area (see Fig. 1) and black solid circles indicate islands and islets in which nests of Kelp Geese and Flightless Steamer-Ducks were present.

little value for explaining variation in the presence of nests of Kelp Geese (Table 3).

The only well-supported model to describe variation in the presence of nests of Flightless Steamer-Ducks on islands contained the explanatory variables of vegetation cover and tourism (Table 2). Both, vegetation cover and tourism had large parameter likelihood values (Table 3), but only vegetation cover had a 95% CI that did not include zero and was present in the top four models. The explanatory variable predators was not well-supported and its model-averaged parameter estimate has a SE larger in magnitude than the actual estimate (Table 3).

TABLE 1. Mean ± SE and, in parenthesis, minimum and maximum values of habitat attributes of nesting sites of Kelp Geese (n = 37) and Flightless Steamer-Ducks (n = 17).

Habitat characterisitics	Kelp Geese	Flightless Steamer Ducks
Tree cover within 1 m (%)	1.3 ± 1.3 (0, 50)	0 ± 0 (0, 0)
Shrub cover within 1 m (%)	53.4 ± 5.4 (0, 100)	84.1 ± 5.0 (50, 100)
Grass cover within 1 m (%)	34.6 ± 5.2 (0, 90)	12.3 ± 4.7 (0, 50)
Bare (%)	10.7 ± 3.4 (0, 100)	3.5 ± 3.0 (0, 50)
Distance to high-tide line (m)	11 ± 1.0 (1, 40)	17.1 ± 3.0 (2, 50)
Altitude above sea level (m)	4.6 ± 0.7 (0, 19)	6.4 ± 0.9 (2, 12)
Slope (degrees)	16.5 ± 1.3 (7, 43)	17.1 ± 1.7 (9, 35)

TABLE 2. Generalized linear models evaluating variation in the presence of nests of Kelp Geese and Flightless Steamer-Ducks on islands and islets of the Beagle Channel. K, number of estimated parameters; AIC_c, Akaike's information Criterion corrected for small samples; ΔAIC_c, differences in AIC_c; w_i, Akaike weight. All candidate models and the null model are presented, listed in decreasing order of ΔAIC_c. The explanatory variables are vegetation cover (low, high), predators (present, absent), and tourism (present, absent).

Response variable	Model	K	AIC_c	ΔAIC_c	w_i
Presence of Kelp Goose nests	vegetation cover + predators	3	46.80	0.00	0.45
	vegetation cover + predators + tourism	4	47.61	0.81	0.30
	vegetation cover	2	50.82	4.03	0.06
	predators + tourism	3	51.23	4.43	0.05
	predators	2	51.36	4.56	0.05
	null	1	51.58	4.78	0.04
	tourism	2	52.25	5.45	0.03
	vegetation cover + tourism	3	52.33	5.53	0.03
Presence of Flightless Steamer-Duck nests	vegetation cover + tourism	3	34.96	0.00	0.61
	vegetation cover + predators + tourism	4	37.44	2.48	0.18
	vegetation cover	2	37.83	2.87	0.14
	vegetation cover + predators	3	39.94	4.98	0.05
	tourism	2	43.26	8.29	0.01
	predators + tourism	3	43.38	8.42	0.01
	predators	2	46.80	11.84	0.00
	null	1	47.95	12.98	0.00

DISCUSSION

It is remarkable that nests of Kelp Geese and Flightless Steamer-Ducks were observed only on islands and islets of the Beagle Channel. This finding contrasts observations on Navarino Island (Schüttler et al. 2009), on the opposite coast of the channel, where nests of Flightless Steamer-Ducks have been found in surveys conducted during the breeding seasons 2005–2006 and 2006–2007. One difference between these two coasts is that the American mink arrived in the IGTF in the late 1940s and was first recorded on the coast of the Beagle Channel in 1990 (Lizarralde and Escobar 2000); whereas in Navarino, there were no records of mink until 2001 (Jaksic et al. 2002, Rozzi and Sherriffs 2003). Another difference is that in the IGTF, native terrestrial predators were present even before mink introduction; whereas, Navarino Island lacks native terrestrial mammalian predators. Several ground predators have been recorded in the study area of the IGTF, such as the introduced American mink and the South American grey fox, the native huillín or southern river otter and the Fuegian culpeo fox, and feral dogs

TABLE 3. Parameter likelihoods, weighted parameter estimates ± unconditional standard error (SE), and 95% confidence interval limits (CL) for explanatory variables describing variation in the presence of nests of Kelp Geese and Flightless Steamer Ducks on islands and islets in the Beagle Channel. Explanatory variables with CL excluding zero are in bold.

Response variable	Explanatory variable	Parameter likelihood	Parameter estimate ± SE	CL	
				Lower	Upper
Presence of Kelp Goose nests	Intercept		−0.57 ± 0.68	−1.90	0.76
	Vegetation cover[a] high	**0.84**	**1.96 ± 0.92**	**0.16**	**3.77**
	Predators[b] present	**0.84**	**−2.79 ± 1.39**	**−5.52**	**−0.07**
	Tourism[c] present	0.41	−1.07 ± 0.87	−2.78	0.64
Presence of Flightless Steamer Duck nests	Intercept		−2.25 ± 1.14	−4.49	−0.008
	Vegetation cover[a] high	**0.98**	**3.09 ± 1.23**	**0.67**	**5.5**
	Predators[b] present	0.24	0.39 ± 1.20	−1.95	2.74
	Tourism[c] present	0.80	−2.24 ± 1.27	−4.92	0.07

[a] Vegetation cover is a categorical variable (high, low) with low as the reference value.
[b] Predators is a categorical variable (present, absent) with absent as the reference value.
[c] Tourism is a categorical variable (present, absent) with absent as the reference value.

(*Canis lupus familiaris*) (Massoia and Chébez 1993, Lizarralde and Escobar 2000, Gomez et al. 2010). In our study area, the huillín feeds mainly on marine resources and its distribution is rather patchy along the IGTF coast, but the more distributed mink and both fox species are generalists and include seabirds in their diet, among other prey items (Gomez et al. 2010, Valenzuela et al. 2013b). Of these predators, the American mink, the huillín, and the Fuegian culpeo fox have been recorded only on six out of 36 of the surveyed islands and islets of the Beagle Channel (4 islands with mink, 1 island with mink and huillín, 1 island with mink and fox). Therefore, islands and islets of the Beagle Channel provide a relatively safe nesting habitat for Kelp Geese and Flightless Steamer-Ducks compared to the coast of the IGTF.

During our surveys on the IGTF, and consistent with other studies (Raya Rey and Schiavini 2002), we did find adult Flightless Steamer-Ducks and Kelp Geese on the beach or swimming in protected bays, but no nests were found. Historically, Flightless Steamer-Ducks have been reported to nest on the coasts of the IGTF (Humphrey et al. 1970, Weller 1975), when the populations of the two introduced predators (American mink and South American grey fox, introduced to the IGTF in the late 1940s; Atalah et al. 1980, Fabbro 1989, Lizarralde and Escobar 2000) along the coast were incipient and when levels of human disturbance were lower. Experimental predator removal studies in the outer archipelago of the Baltic Sea have shown that predation by mink can have locally limiting effects on the breeding densities and community structure of waterfowl (Nordström et al. 2002), and can markedly affect the distribution of bird species (Nordström and Korpimäki 2004). The absence of nests of Kelp Geese and Flightless Steamer-Ducks on the IGTF, but their presence there in the past, suggests that introduced predators may be responsible, in part, for these changes. Additionally, habitat changes caused by increased human disturbance may also explain the absence of both species on the IGTF. Human presence can lead to restricted access to resources such as nesting sites (which occurs through animals avoiding areas where humans are present), and could result in changes in the quality of sites. Along the Argentinean coast of the Beagle Channel in the IGTF, many areas are highly urbanized, and those habitats are now used for industries, construction, livestock grazing, tourism, and recreational activities. Also from our surveys, we know that island habitats are represented along the coast of the IGTF, but unfortunately we have no qualitative data on changes in vegetation cover as a result of human activities. Further work measuring changes in habitat variables (e.g., vegetation cover along the coast of the IGTF) and experimental studies such as those conducted by Nordström et al. (2002) and Nordström and Korpimäki (2004) are needed to assess the effects of human disturbance and introduced predators on the abundance and distribution of coastal breeding bird species on the IGTF.

Several human activities take place along the coast of the IGTF, including recreational activities and tourism, together with increased urbanization affecting the coast. On the other hand, many of the islands and islets of the Beagle Channel, unlike other islands which may be more remote or inaccessible, are also subject to intense human activity from daily tourist boat visits.

Islands provide a relatively safe place for nesting, because they generally offer greater protection against ground predators and human disturbance than continental sites (Lack 1968). Islands and islets of the Beagle Channel are not far from the coast of the IGTF (distances range between 0.1–7 km) where ground predators are more abundant. However, the lack of fresh water sources (in all but one of the islands), the reduced island coastline (median perimeter of islands is 0.6 km, compared for example to the 2–5 km home range of mink; Harrington et al. 2009), and the scarce food resources during winter may prevent ground predators from establishing year-round on these islands even though they could potentially reach them. Therefore, islands of the Beagle Channel may offer more protection against ground predators compared to the IGTF, but not all of them necessarily offer more protection against human disturbance.

Our study showed that vegetation cover was an important variable in explaining the variation in the presence of nests of Flightless Steamer-Ducks and Kelp Geese on islands. Actually, nests were absent on islands with low vegetation cover. This finding agrees with previous studies in the area which have also found nests of Flightless Steamer-Ducks and Kelp Geese to be associated with bushes or other concealment (Humphrey et al. 1970, Clark 1984). This is consistent with a study on a related species along the coast of Chubut, Patagonia, Argentina (Agüero et al. 2010), where nesting sites of White-headed

Steamer-Ducks (*Tachyeres leucocephalus*) were positively associated with higher proportions of shrub vegetation cover. One advantage of vegetation cover is increased concealment from predators, and its importance differs depending on the type of predator (e.g., Clark and Nudds 1991, Butler and Rotella 1998, Opermanis et al. 2001). Avian predators visually locate nests; whereas, mammalian predators depend on olfactory cues and may prey upon nests regardless of their concealment (Guyn and Clark 1997, Shüttler et al. 2009). Hence, in the majority of ground-nesting birds, vegetation may provide protection mostly from avian predators (Clark and Nudds 1991). On islands off the coast of Chubut province in Argentina, Kelp Gulls (*Larus dominicanus*) and Southern Caracaras (*Caracara plancus*) were observed taking eggs of White-headed Steamer-Ducks, which also select nest sites with higher proportion of shrub vegetation (Agüero et al. 2010). Though we did not observe any avian predators taking eggs of Flightless Steamer-Ducks or Kelp Geese in our study area, several potential avian predators breed on the islands such as Kelp Gulls, Dolphin Gulls (*Leucophaeus scoresbii*) and Chilean Skuas (*Stercorarius chilensis*) (Schiavini and Yorio 1995, Raya Rey and Schiavini 2000). Another advantage of vegetation cover is related to thermal properties of the nests; those shielded by plants have increased protection from wind and reduced convective heat loss (Gloutney and Clark 1997). These risks may be especially important under the ambient conditions experienced in the Beagle Channel area, where average ambient temperature during the breeding season ranges between 5–13 °C and winds have an average speed of 31 km/hr (Bujalesky 2007).

The presence of ground predators was an important factor in explaining the variation in the presence of nests of Kelp Geese on islands; however, it did not have enough support in explaining the variation in the presence of nests of Flightless Steamer-Ducks. This is consistent in part with a study on Navarino Island, south of the IGTF, which suggests that species nesting solitarily, in coastal habitat with rocky outcrop shores and concealed nests, such as Kelp Geese and Flightless Steamer Ducks, are most vulnerable to predation by minks (Schüttler et al. 2009). The differences we found between Kelp Geese and Flightless Steamer-Ducks may be related to differences in the type of vegetation cover at their nest sites. Though mammalian predators may depend primarily on olfactory cues, and therefore prey on nests irrespective of their concealment (Guyn and Clark 1997), other authors have suggested that tall, dense vegetation acts as a visual and scent barrier between nests and predators (Duebbert and Kantrud 1974, Duebbert and Lokemoen 1976, Livezey 1981, Hines and Mitchell 1983) and restricts mammalian movement (Schrank 1972). Several studies demonstrated that nest predation by mammalian predators decreased with increased lateral cover density and understory height (Crabtree et al. 1989, DeLong et al. 1995). Similarly, Johnson et al. (2005) suggest that higher vertical cover may help protect nests from avian predators, and that higher lateral cover may conceal nests from mammalian predators. If so, and considering that the percentage of shrub cover was higher for nests of Flightless Steamer-Ducks than for those of Kelp Geese (Table 1), a greater vegetative scent barrier may better protect Flightless Steamer-Ducks than Kelp Geese from ground predators. Alternatively, the reason why predators are important in explaining variation in the presence of nests of Kelp Geese on islands but not of nests of Flightless Steamer-Ducks may be related to the highly aggressive behavior of the latter species. Steamer-ducks are known to be strongly aggressive towards their own and other species (Weller 1976; Livezey and Humphrey 1985; ARR, pers. obs.), and many instances of interspecific aggression by steamer-ducks can be explained as anti-predator actions (Livezey and Humphrey 1985).

Our study provides new information on the breeding habitat and nesting sites of Kelp Geese and Flightless Steamer-Ducks in the Beagle Channel, which in the future may contribute to the identification of priority breeding sites, habitats, and specific habitat features to protect. Further research trying to identify their main nest predators, examining to what extent nest predation might influence the breeding success of Kelp Geese and Flightless Steamer-Ducks, and determining if vegetation cover of the nests influences breeding success would provide greater knowledge on the biology of these poorly studied species. Finally, the absence of nests of Kelp Geese and Flightless Steamer-Ducks on the coast of the IGTF but their presence there in the past, when levels of human disturbance and when the population of introduced predators was lower, suggests that introduced predators, human dis-

turbance, and coastal development may be responsible, in part, for these changes. In this context, it is important to highlight the importance of islands and islets of the Beagle Channel as a safe breeding refuge for these two ground nesting seabirds.

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BREEDING BIOLOGY OF COAL-CRESTED FINCHES

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ABSTRACT.—The Coal-crested Finch (*Charitospiza eucosma*) is a rare, globally near threatened and poorly known species, endemic to the savannas of central Brazil and Bolivia. We investigated this species' breeding biology in the Brazilian savannas between 2008–2010. We found 44 nests of Coal-crested Finches during one and a half breeding seasons. Coal-crested Finches reproduced in two discrete peaks within the rainy season (i.e., bimodal breeding). Nests were cup-shaped and built on trees with a mean height of 2.18 ± 1.34 m (n = 42). Modal clutch size was 2 (range = 1–3). Eggs averaged 16.32 ± 1.16 mm (length; n = 46), 11.30 ± 1.06 mm (width; n = 46) and 1.40 ± 0.14 g (mass; n = 44). Incubation and nestling periods lasted on average 13.4 ± 0.42 days (n = 5) and 12.0 ± 2.63 days (n = 7), respectively. Young (0–4 days old), middle-aged (5–9 days old) and late nestlings (10–13 days old) weighed from 1.25–6.35 g (n = 10), from 5.30–12.65 g (n = 12) and from 9–11.90 g (n = 9), respectively. Estimated nesting success was 20.08% (n = 38). The Coal-crested Finch has similarities (e.g., nest material, clutch size, eggs, nestling period, nestlings and nesting success) and differences (e.g., nest structure, nest sites, incubation period, breeding season) with other Neotropical finches. We suggest that their bimodal breeding season may have evolved in response to two annual peaks of food resource abundance: arthropods followed by grass seeds. *Received 11 October 2012. Accepted 4 April 2013.*

Key words: biannual breeding, breeding ecology, finches, Neotropical birds, nesting biology.

The breeding biology of Neotropical oscines remains largely unknown (Martin et al. 2000, Sick 1997, Stutchbury and Morton 2001, Auer et al. 2007). The Coal-crested Finch (*Charitospiza eucosma*) is a species from a monotypic genus (Remsen et al. 2012), restricted to the savannas (''Cerrado'') of central Brazil and Bolivia (Bates et al. 1992, Ridgely and Tudor 1989, Sick 1997), with unclear phylogenetic relationships within the Emberizidae and Thraupidae (Sibley and Monroe 1990, Remsen et al. 2012). The species is considered globally near threatened (BirdLife International 2012). The nest was only recently described from a fragment of savanna in central Brazil (Borges and Marini 2008). Therefore, information about their breeding biology may be useful for conservation management strategies and to understand its relationship within the complex of ''New World nine-primaried oscines'' (Bledsoe 1988, Klicka et al. 2000).

In this study we present details of the breeding biology of Coal-crested Finches, including descriptions of breeding season, nest sites, nest morphology, clutch size, eggs, nestlings, the duration of both incubation and nestling periods, and nesting success.

METHODS

Study Area and Period.—The study was conducted in a 250.53 ha patch within a 82,679.88 ha savanna and grassland (referred to as ''Cerrado'') conservation unit—APA *da bacia do Rio São Bartolomeu*—in central Brazil (15° 40′ S, 47° 43′ W). The selected patch is composed entirely of Cerrado vegetation, including native grasses; it is located near rural farms and often disturbed by logging. There is scattered occurrence of exotic grasses *Brachiaria* spp. and *Melinis* spp. inside the study site and *Andropogon gayanus* at the edges. The study site was burned (<1 year) prior to the start of this study. This study was conducted continuously between June 2008–December 2009, when we searched for nests at least once a week. We also searched sporadically for nests in January, February and October 2010. Local climate is classified as humid tropical (Aw) (Köppen 1948), with two well defined seasons: rainy summer and dry winter (Fig. 1).

Data Collection.—We conducted nonsystematic observations with individuals looking for evidence of reproductive activity (e.g., territoriality behavior, courtship, nest building) during the study period. We only looked for nests in sites usually used by this species, i.e., shrubs and trees in typical savanna habitat (Borges and Marini 2008). In order to accurately estimate the duration

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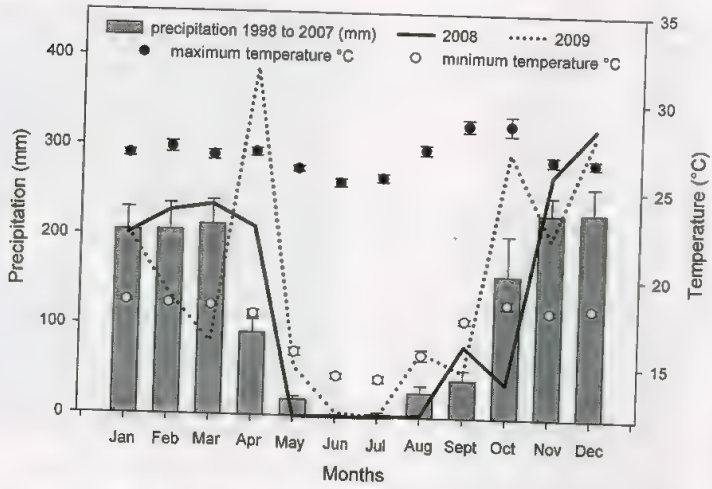

FIG. 1. Monthly precipitation and temperature in the study site previous to (1998–2007) and during the study period (2008-2009, rainfall only; continuous and dashed lines). The mean (± SE) of rainfall (gray bars) and maximum and minimum temperatures (scatter plots) are shown. Data from Weather Station of Embrapa Cerrados (Distrito Federal).

of the breeding season, we did not consider nests found outside of the continuous monitoring period.

We monitored nests at intervals ranging from 1–5 days (mean ± SD = 2.48 ± 1.17 days, n = 198). During each monitoring section, we recorded nest status (active or inactive), the presence and number of eggs or nestlings, and the presence of any parent incubating or within the territory near the nest. We avoided checking the nests when the females were incubating (egg stage) or when a parent was on the edge of the nest (nestling stage) (Mayer-Gross et al. 1997); in such cases, we returned later on the same day to check the nest. The incubation period of each nest was considered to be the time between the last egg laid and first egg hatched, and the nestling period was the period between hatching of the first egg and the last young to fledge. We considered the activity period of a nest as the interval between egg laying and fledging. We estimated dates of egg laying, hatching and fledgling by assuming average days between checks (Mayfield 1961, 1975). We were able to determine the exact nestling period (14 days) of one nest only.

We recorded plant species where the nests were found, the shape of the nests (*sensu* Simon and Pacheco 2005) and the materials used to build them. We also measured nests' height above the ground and the height, internal and external diameters, and depth of the nests. Nest height above the ground was measured with a 3-m tape (0.1-cm accuracy), and the measurements of the nest structure were taken using a caliper (0.1-mm accuracy).

We estimated the clutch size and egg-laying synchrony based only on those nests we found under construction or with only the first egg laid (n = 16). We described the color and shape, and measured eggs' length, width (caliper: 0.1-mm accuracy) and mass (dynamometer: 0.01-g accuracy). We described nestlings' morphology by recording the color and distribution of body plumage, and measuring nestlings' mass (dynamometer: 0.1-g accuracy).

Data Analyses.—We estimated the dates that the nests failed by using the mean date of nest checking (Mayfield 1961, 1975). We estimated nesting success by using the Mayfield method—considering the rates of daily nest survival (DSR) and nest survival probability (Mayfield 1961, 1975). We also estimated the variance and standard deviation of nests' daily survival rates (Miller and Johnson 1978, Johnson 1979). We compared DSRs between incubation and nestling period with a z test (Johnson 1979).

We tested whether the phenological distribution of the nests was uniform within the breeding season and throughout the year, using the Rayleigh test. Additionally, we compared the phenological distribution of the nests between the two breeding peaks occurring in the same breeding season with the Mardia-Watson-Wheeler

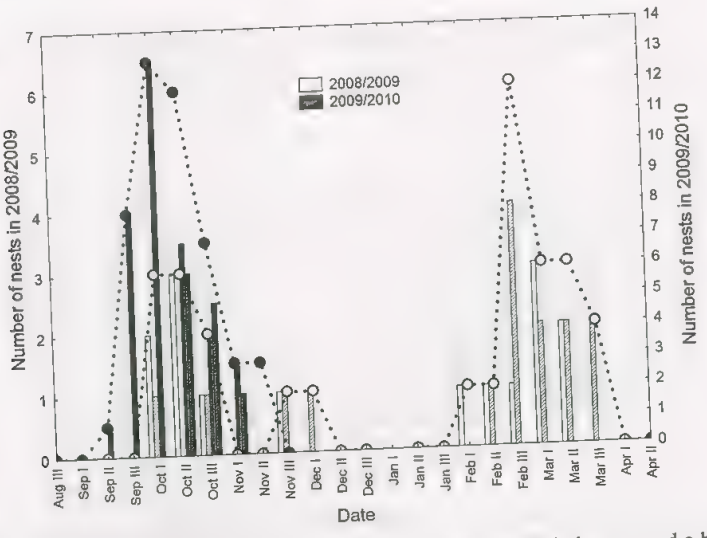

FIG. 2. Nesting season of the Coal-crested Finch population in central Brazil during one and a half breeding seasons (from Oct 2008–Dec 2009). Empty bars indicate the nests with eggs and cross-hatched bars indicate nests with nestlings. Circles indicate the total active nests.

test (Zar 2010). We used Oriana 4.01 (Kovach 2011) software for phenological analysis and R 2.15.1 for the remaining analysis. For all descriptive statistics, means are displayed followed by ± SD.

RESULTS

We found 44 nests of Coal-crested Finches from October 2008 to December 2009. We found two additional nests in January and February 2010 and two in October 2010.

Considering only the 2008–2009 breeding season, it showed two discrete peaks, the first from September to December 2008, and the second from February to March 2009, both during the rainy season (Fig. 2). The first breeding peak lasted 65 days and the second 46 days, with an interval between peaks of 60 days. The phenological distribution of nests was non-uniform (i.e., seasonal) throughout the year (average date = 23 Jan ± 60 days; Rayleigh, $Z = 25.536$, $P < 0.001$, $n = 111$) and within that breeding season (average date = 12 Dec ± 71 days; Rayleigh, $Z = 38.35$, $P < 0.001$, $n = 111$). The phenological distribution of nests differed between breeding peaks (Mardia-Watson-Wheeler test, $W = 85.34$, $P < 0.001$; first peak 28 Oct ± 23 days; second peak 4 Mar ± 13 days).

Coal-crested Finches nested in 11 different tree taxa ($n = 38$ individual trees identified): *Qualea* spp. trees ($n = 12$ nests), *Q. parviflora* ($n = 10$), *Q. grandiflora* ($n = 3$), *Ouratea hexasperma* ($n = 7$), *Byrsonima* spp. ($n = 5$), *Eriotheca pubescens* ($n = 3$), *Erythroxylum* spp. ($n = 3$), *Palicourea rigida* ($n = 3$), *Aspidosperma tomentosum*, *Annona crassiflora*, *Eremanthus glomerulatus*, and *Vochysia thyrsoidea* (one nest on each). Nests were built in forks at 2.18 ± 1.34 m above the ground (range = 0.32–7.62 m, $n = 42$).

Based on occasional observations made during searching and monitoring, we recorded both males and females building the nests. Nests presented a low/cup fork shape and were built with petioles, rachis of grass, spider webs, silk, cotton, and fine roots. Nests averaged 35.42 ± 5.16 mm in depth (range = 23.25–44.72, $n = 27$), 38.03 ± 4.43 mm in height (range = 30.72–45.60 mm, $n = 27$), 64.79 ± 5.30 mm in external diameter (range = 52.05–74.81 mm, $n = 28$) and 45.29 ± 4.15 mm in internal diameter (range = 35.40–53.88 mm, $n = 28$). After inactivation of the nests, we observed a reduction in the amount of material in these nests, which may indicate re-use of nest material.

Females laid each egg with 1 ($n = 7$) or 2 day ($n = 1$) intervals. Only females incubated the eggs ($n = 72$ observations). Incubation periods lasted on average 13.4 ± 0.42 days (range = 13.0–14.0 days, $n = 5$). Modal clutch size was two eggs (range = 1–3 eggs, $n = 16$). Eggs had pyriform, conical, longitudinal or oval shapes (Sick 1997) and were blue-green with many brown stains concentrated on the obtuse pole, forming a subterminal ring (Fig. 3). Mean length of the eggs was 16.32 ± 1.16 mm ($n = 46$ eggs), width was

FIG. 3. Nest and eggs of the Coal-crested Finch.

11.30 ± 1.06 mm (n = 46) and mass was 1.40 ± 0.14 g (n = 44). Eggs hatched synchronously (n = 1) or with a one-day interval (n = 1). Nestling period averaged 12.0 ± 2.63 days (range = 7.5–15.0 days, n = 7). Nestlings (0–4 days old) hatched with closed eyes and few light grey feathers irregularly distributed on the upper and lower limbs, backs, bellies, and eyebrows, and weighed 1.25–6.35 g (n = 10). Middle-aged nestlings (5–9 days old) had open eyes, bare heads, numerous feathers on the sides of the body, long calamus (remiges, rectrices, wings and back) and weighed between 5.30–12.65 g (n = 12). Late nestlings (10–13 days old) had predominantly bare heads; white (belly) and orange buff (back) feathers hidden in the center of the chests, bellies, cloacae and flanks; incipient tails; and weighed between 9–11.90 g (n = 9). We observed parasitism by insect larvae (n = 21) (probably *Philornis* spp.: Diptera) in 26.19% of the nestlings (n = 42) and 36.37% of the broods (n = 22). Fledging was synchronous (n = 3 nests) or on consecutive days (n = 3).

Overall daily survival rate (DSR) and nest survival probability were, respectively, 0.939 ± 0.012 (424.5 nest-days) and 20.08% (n = 38). Nests were unsuccessful because of predation (53.85%), abandonment during incubation stage (19.23%), or unidentified causes (26.92%). Daily survival rates did not differ between incubation (DSR 0.932 ± 0.016) and nestling stages (DSR 0.94 ± 0.019 SD; z-test, Z = 0.33, P = 0.37).

DISCUSSION

Some aspects of the breeding biology of the Coal-crested Finches were in accordance with the pattern for the closely related Thraupidae and Emberizidae (taxonomy according to Remsen et al. 2012). First, the low cup shape of the nests of Coal-crested Finches is common in closely related Neotropical species (Sick 1997, Mezquida 2003, Francisco 2006, Lima and Buzzetti 2006, Gressler and Marini 2011; but see Biancucci and Martin 2008, Braz 2008), as well as the materials used in nest building, including stems and grass roots (Mezquida 2003, Mezquida and Marone 2003, Francisco 2006, Marini et al. 2007, Gressler and Marini 2011), petioles (Mezquida 2003), "sticks" (Greeney et al. 1998, Biancucci and Martin 2008), spider webs (Francisco 2006, Rovedder and Fontana 2012), plant fibers (Rovedder and Fontana 2012), and silk cotton (Mezquida 2003).

In accordance with the pattern of latitudinal gradient on avian clutch size (Griebeler et al. 2010), the clutch size of the Coal-crested Finches was similar to the clutch size of other Neotropical species (1–3 eggs; de Medeiros and Marini 2007; Marini et al. 2009a, b; dos Santos and Marini 2010; Duca and Marini 2011) and closely related species (1–3 eggs; Skutch 1985; Francisco 2006, 2009; Gressler and Marini 2011; Rovedder and Fontana 2012), and different in relation to closely related southern species which have clutch sizes between 3–4 eggs (Mason 1985, Mezquida 2003, Mezquida and Marone 2003). Laying was asynchronous in Coal-crested Finches as observed in closely related Neotropical species (Skutch 1985, Francisco 2006, Carvalho et al. 2007).

Egg color varies across Neotropical finches and relatives (Ridgely and Tudor 1989, Sick 1997). The greenish-blue eggs of the Coal-crested Finch are found in some Neotropical related species (Williams 1981; e.g., Stripe-tailed Yellow Finch, *Sicalis citrina*, Gressler and Marini 2011), but many others have eggs of different colors (Oppel et al. 2003; Francisco 2006, 2009; Greeney 2009; e.g., *Emberizoides* spp. Rodrigues et al. 2009), such as white with reddish-brown spots (Lima and Buzzetti 2006, Biancucci and Martin 2008, Braz 2008; e.g., Warbling Finch, *Poospiza cinerea*, Wischhoff et al. 2012). Relative egg mass (egg mass/body mass ratio) of the Coal-crested Finch (0.13) is intermediate compared to the small-sized related Neotropical species, such as the Stripe-tailed Yellow Finch (0.13; Gressler and Marini 2011), the Ochre-breasted Brush-Finch (*Atlapetes semirufus*) (0.11; Biancucci and Martin 2008), the Double-collared Seedeater (*Sporophila caerulescens*) (0.15; Francisco 2006) and the Blue-black

Grassquit (*Volatinia jacarina*) (0.15; Carvalho et al. 2007) (Dunning 2007).

Nestling morphology and mass of the Coal-crested Finch were in accordance with a pattern of small Neotropical Emberizidae nestlings (Mason 1985, Mezquida and Marone 2000). Nestling period of Coal-crested Finches (12 days) is intermediate for a Neotropical finch (Mason 1985, Mezquida 2003, Francisco 2006, Greeney 2009, Gressler and Marini 2011; e.g., 10 days in Blue-black Grassquits, Carvalho et al. 2007; 14 days in Rufous-collared Sparrow, *Zonotrichia capensis*, Auer et al. 2007). However, we measured the body mass of nestlings in the same nests that we estimated nestling periods, and this may have underestimated the period of nestlings because of handling disturbance (Parsons and Burger 1982).

Nesting success of the Coal-crested Finches (20%) is within the range found in both Neotropical related species (Mezquida and Marone 2001) and other species with open cup nests, such as the sympatric Stripe-tailed Yellow-Finch (21.2%; Gressler and Marini 2011). Predation was the main cause of nest loss, but the proportion of abandoned nests was higher in Coal-crested Finches (19.23%) than in other Neotropical passerines with open cup nests (Mezquida and Marone 2000, 2001; Marini et al. 2009a; e.g., 11.8% in Gray-hooded Flycatcher, *Mionectes rufiventris*; Aguilar et al. 2000). Many hypotheses have been proposed to explain the ultimate causes of nest abandonment, for example, trade-offs in life history (Verboven and Tinbergen 2002), sexual conflicts (Pogány et al. 2008) and unpredictability of food availability (Sergio et al. 2011). Coal-crested Finches could be a useful species to test these hypotheses about the intensity of nest abandonment.

Although there were several similarities between the reproductive patterns of the Coal-crested Finch and the other related species, their breeding patterns are distinguished in many aspects from Neotropical Emberizidae in open habitats. Although Neotropical finches usually build nests near the ground in herbaceous plants and shrubs (Sick 1997, Auer et al. 2007, Biancucci and Martin 2008, Braz 2008, Gressler and Marini 2011; e.g., Blue Finch, *Porphyrospiza caerulescens*, Lima and Buzzetti 2006), Coal-crested Finches nested higher (~2.18 m) in the savanna taxa of trees, common in central Brazil (Felfili and da Silva 1993, Assunção and Felfili 2004, Aquino et al. 2007). Nests of Coal-crested Finches are wide (low height/external diameter ratio: 0.59) (Contino 1968, Mezquida 2003, Francisco 2006, Lima and Buzzetti 2006, Auer et al. 2007, Biancucci and Martin 2008, Braz 2008; e.g., 0.78 in Stripe-tailed Yellow-Finch, Gressler and Marini 2011) and have longer incubation periods (13.4 days) than many other nests of Neotropical finches (Francisco 2006, Carvalho et al. 2007, Gressler and Marini 2011; e.g., 12 days in Common Diuca-Finch, *Diuca diuca*, Mezquida 2003; but see Mason 1985). It is possible that Coal-crested Finches have higher survival rates than related species, because long incubation periods may reduce the risk of the parents' mortality, in spite of increasing the period of nest exposure to threats such as nest predators (Martin 2002). However, this hypothesis remains untested and should be considered in further studies.

The most unexpected aspect of the breeding biology of the Coal-crested Finches was their long and bimodal breeding season with two remarkable and discrete peaks during an interval <1 year. The bimodal pattern of breeding is rare for birds but may be less uncommon for tropical birds, especially those that occur in equatorial habitats (Moreau 1950, Miller 1962, Wilkinson 1983, Schondube et al. 2003, Greeney 2010). Research suggests that bimodal breeding is related to the bimodal distribution of precipitation, which in turn may lead to bimodal peaks of food supply (reviewed in Schondube et al. 2003). For example, bimodal breeding for the omnivorous Yellow-faced Grassquit (*Tiaris olivaceus*) can be synchronized with two peaks of availability of different resource types (grass seeds and fleshy fruits; Skutch 1950). Likewise, the Coal-crested Finch is an omnivorous species, feeding mainly on grass seeds and insects (PD, unpubl. data), and may have breeding peaks parallel to the distribution of these two types of food resources. The peak of arthropod abundance in savannas and grasslands of central Brazil occurs between September and December (da Silva et al. 2011), a period that corresponds to the first breeding peak of the Coal-crested Finch (see Results) and to the breeding season of most other insectivorous bird species (Gressler and Marini 2007; de Medeiros and Marini 2007; Sousa and Marini 2007; Braz 2008; França and Marini 2009; Marini et al. 2009a, b; dos Santos and Marini 2010; Duca and Marini 2011). Additionally, the peak in abundance of grass seeds in savannas and grass-

lands of central Brazil occurs between January and March (Munhoz and Felfili 2005, Ramos 2010), period of occurrence of the second breeding peak of the Coal-crested Finch (see Results) and of the breeding season of some sympatric granivorous bird species (Francisco 2006, Carvalho et al. 2007, Gressler and Marini 2011). Therefore, we suggest that bimodal breeding in the Coal-crested Finch may have evolved in response to two annual peaks in the availability of distinct types of resources. Further studies should try to confirm these hypotheses about the evolution of bimodal breeding in omnivorous bird species.

In this study, we described several traits of the breeding biology of Coal-crested Finches (length of breeding season, nests, eggs and nestlings, incubation and nestling periods, and nesting success). Our results may contribute to future demographic and population genetics studies and be useful for conservation management of this endemic and near-threatened species. We also emphasize the occurrence of bimodal breeding in Coal-crested Finches, a rare and poorly known breeding season system in birds.

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CURRENT DISTRIBUTION AND ABUNDANCE OF THE O'AHU 'ELEPAIO (*CHASIEMPIS IBIDIS*)

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ABSTRACT.—The O'ahu 'Elepaio (*Chasiempis ibidis*) is an endangered monarch flycatcher endemic to the Hawaiian Island of O'ahu. Current information on abundance, distribution, and population trend is needed to help assess the species status and identify areas where conservation efforts can be focused. We used spot-mapping methods with song playbacks to conduct surveys in the Ko'olau Mountains from 2011–2012, and we used occupancy sampling with repeated visits to estimate detection probability. We detected 545 male and 317 female O'ahu 'Elepaio. The detection probability of males was 0.92 ± 0.03 and that of females was 0.86 ± 0.05, yielding corrected estimates of 592 males (95% CI = 554–630) and 369 females (95% CI = 327–411). Combined with results of a previous census in the Wai'anae Mountains that found 192 males and 84 females, the total estimated population of the species is 1,261 birds (95% CI = 1,205–1,317), consisting of about 477 breeding pairs and 307 single males. The O'ahu 'Elepaio has declined in abundance by about 50% since the 1990s, when the population was estimated to be about 1,974 birds. The current geographic range of the O'ahu 'Elepaio encompassed about 5,187 ha and has declined by 75% since 1975, becoming fragmented into four larger subpopulations with 100 or more birds each and 12 smaller subpopulations. Rat control to reduce nest predation remains the cornerstone of the conservation strategy for the O'ahu 'Elepaio, but variation in forest structure, forest dynamics, and continuing evolution of 'elepaio nesting behavior are likely to play important roles in determining whether this species can persist. *Received 24 January 2013. Accepted 20 March 2013.*

Key words: abundance, detection probability, Hawai'i, O'ahu 'Elepaio, range.

The O'ahu 'Elepaio (*Chasiempis ibidis*) is a territorial, non-migratory monarch flycatcher (Monarchidae) endemic to the island of O'ahu in the Hawaiian Archipelago (VanderWerf 1998). 'Elepaio also occur on Kaua'i and Hawai'i, and the forms on each island were treated as subspecies for many years, but morphological, behavioral, and genetic evidence indicate 'elepaio on each island constitute separate species (Conant et al. 1998; VanderWerf 2007, 2012a; VanderWerf et al. 2010). In 2010, the American Ornithologists' Union changed the taxonomy so that each island form is recognized as a distinct species (Chesser et al. 2010, VanderWerf 2012c). The Kaua'i 'Elepaio (*C. sclateri*) and Hawai'i 'Elepaio (*C. sandwichensis*) are fairly common and widespread (Scott et al. 1986, Gorresen et al. 2009), but the O'ahu 'Elepaio is rare and locally distributed, is listed as endangered under the U.S. Endangered Species Act (USFWS 2000, 2006) and by the State of Hawai'i, and is considered endangered by the International Union for the Conservation of Nature (IUCN 2012).

The O'ahu 'Elepaio was abundant and widespread in forested habitat throughout the island in early 20th century (Seale 1900, Perkins 1903, Bryan 1905), but it has declined steadily and in the 1990s it was estimated to occupy <4% of its presumed prehistoric range and <25% of the range occupied in 1975 (VanderWerf et al. 2001). The island-wide population was estimated to be 1,974 birds based on surveys conducted during the 1990s (VanderWerf et al. 2001). Roughly half of the total population was found in the Wai'anae Mountains of western O'ahu and half was found in the Ko'olau Mountains of eastern O'ahu. A more recent census in the Wai'anae Mountains from 2006–2009 found only 300 O'ahu 'Elepaio, indicating their numbers have continued to decline (VanderWerf et al. 2011a), but the recent population trend in the Ko'olau Mountains is unknown.

The primary threats responsible for the decline of the O'ahu 'Elepaio are nest predation by alien black rats (*Rattus rattus*) and mosquito-borne diseases (VanderWerf 2001, VanderWerf and Smith 2002, USFWS 2006, VanderWerf et al.

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2006, VanderWerf 2009). Controlling transmission of mosquito-borne avian diseases in Hawai'i has been very difficult (LaPointe et al. 2009), but rat control has proven to be an effective method of increasing O'ahu 'Elepaio nest success and survival of breeding females, if properly implemented, and has become the cornerstone of the conservation strategy for this species (VanderWerf and Smith 2002, VanderWerf 2009, VanderWerf et al. 2011b). Ground-based rodent control using snap traps and poison bait stations has been conducted in several areas and by several agencies, and has resulted in modest but localized population increases (VanderWerf 2009, VanderWerf et al. 2011b). Restoration of native forest habitat also may be beneficial to the O'ahu 'Elepaio and could reduce the need for rat control by reducing the abundance of non-native, fruit-bearing trees that support large numbers of rats and attract them into the forest canopy (VanderWerf 2009). More diverse and intact native forest also may support higher abundance and diversity of arthropods that are prey for 'elepaio (VanderWerf 1994, Fretz 2002). The O'ahu 'Elepaio is evolving in response to nest predation by rats through increasing nest height (VanderWerf 2012b), and this natural population response in combination with active management may help to decrease the extinction risk of this species.

The purposes of this study were to: (1) provide current information about the distribution and abundance of the O'ahu 'Elepaio; and (2) identify areas where numbers of 'elepaio are declining and where conservation efforts can be focused. This information can be used by agencies and organizations to help assess the conservation status of the species and coordinate management.

METHODS

We used spot-mapping survey methods with song playbacks to determine the distribution and abundance of the O'ahu 'Elepaio in the Ko'olau Mountains. Surveys consisted of walking up or down a valley or ridge or traversing an area of forest and stopping to play recorded O'ahu 'Elepaio songs at approximately 100-meter intervals. 'Elepaio defend territories year-round and playbacks are an efficient method of locating birds and determining the extent of their territory (Falls 1981, VanderWerf 2004). 'Elepaio often respond more strongly to local song dialects (VanderWerf 2007), so recordings used during playbacks were from the area being surveyed or a nearby area. Each playback lasted approximately 3 secs, after which we watched and listened for approximately 20 secs. We repeated this procedure at least three times, unless a bird responded sooner. Most 'elepaio respond to playbacks within 1 min (VanderWerf 2007), but some birds approach quietly and must be searched for visually. We recorded the age and sex of each 'elepaio observed, any behaviors or association with other 'elepaio, and whether each territory contained a pair or a single male. We recorded the location of detections with a Global Positioning System (GPS) device. Consecutive detections were counted as different individuals if the birds could be distinguished by color bands or distinctive plumage, if birds from neighboring territories were observed simultaneously, or if the detections occurred more than 150 m apart, making it unlikely they were from the same territory. 'Elepaio territory size varies with habitat structure and population density (VanderWerf 2004), but the width of a territory is usually 75–150 m. 'Elepaio may move farther and follow an observer for longer distances in areas where their population density is low. If it appeared that a bird might have been following us, we used additional playbacks to ascertain the extent of its territory to avoid counting it twice.

Although playbacks are effective at increasing the detection probability of 'elepaio, some individuals may not respond to playbacks on a given day, resulting in imperfect detection (MacKenzie et al. 2002). To determine the proportion of birds that we may have missed, we repeated surveys three times in four areas and estimated the detection probability using program PRESENCE2 (Hines 2006). We estimated the detection probability for males and females separately, because males are more likely than females to respond to playbacks (VanderWerf and Freed 2003). We used the resulting detection probabilities to correct our estimates of abundance. We calculated 95% confidence intervals around the corrected abundance estimates by using the delta method to calculate the variance, which results in a narrower interval (Oehlert 1992). The equation for the variance around the population estimate for males and females combined is:

$$\mathrm{var}(N) = \left\{ n_m{}^2 * \sigma_{pm}{}^2 * \left(1/p_m{}^2\right)^2 \right\} + \left\{ n_f{}^2 * \sigma_{pf}{}^2 * \left(1/p_f{}^2\right)^2 \right\}$$

Where n_m and n_f are the numbers of birds detected, σ_{pm} and σ_{pf} are the variances of the detection probabilities, and p_m and p_f are the detection probabilities, for males and females respectively.

Two of the areas we surveyed repeatedly had high densities of ʻelepaio (North Halawa Valley, Pia Valley) and two of the areas had moderate densities (Hawaiiloa Ridge, Wiliwilinui Ridge). For the uncorrected abundance at those sites, we used the highest number of birds detected on any single visit. The proportion of territories in which we detected birds was similar among the three visits for males (mean = 0.92, range 0.91–0.93) and females (mean = 0.60, range 0.55–0.66), indicating there was no systematic pattern or temporal bias in detection probability.

We surveyed almost all areas in the Koʻolau Mountains where Oʻahu ʻElepaio have been reported in the last 40 years (Shallenberger 1977, Shallenberger and Vaughn 1978, VanderWerf et al. 2001), with a few exceptions. We were not able to survey some private lands because we could not obtain permission for access, including Punaluʻu, Kaʻaʻawa, and portions of Waiahole Valley. Several areas we covered had never been surveyed but contained suitable habitat, such as upper Waimalu and Waimano valleys.

To determine the current range of the Oʻahu ʻElepaio, we used a Geographic Information System (GIS) to create a 200-m radius buffer around all points where we detected birds, and then drew a polygon around the buffered points. In cases where we suspected the range did not extend 200 m from the observation point, such as steep cliffs at the head of a valley or a narrow ridge that supported only low vegetation not suitable for ʻelepaio, we drew the polygon to coincide with the limiting geographic or vegetative feature. We used this procedure to measure the geographic range of the Oʻahu ʻElepaio in the Koʻolau Mountains using detections reported in this study, and also using detections reported in the Waiʻanae Mountains of western Oʻahu by VanderWerf et al. (2011a), where the size of the current range has not been measured.

RESULTS

We detected 545 male and 317 female Oʻahu ʻElepaio during surveys in the Koʻolau Mountains from January 2011–June 2012 (Fig. 1). The detection probability of males was 0.92 ± 0.03 and that of females was 0.86 ± 0.05, based on areas that we surveyed on three occasions. Applying the detection probabilities to the numbers of actual detections, and using the delta method to calculate confidence intervals, yielded corrected estimates of 592 males (95% CI = 554–630) and 369 females (95% CI = 327–411), and a total population estimate of 961 (95% CI = 905–1,017). The proportion of paired males was 0.58 overall (Table 1), and was generally higher in and near areas where rats have been controlled, including Wailupe Valley west fork (0.78), Pia Valley (0.82), and Kupaua Valley (0.88).

The geographic range of the Oʻahu ʻElepaio encompassed a total of 5,187 ha (12,811 ac) in 2011–2012, including 3,948 ha (9,749 ac) in the Koʻolau Mountains and 1,239 ha (3,060 ac) in the Waiʻanae Mountains (Table 2, Fig. 2). In the Koʻolau Mountains, the range was fragmented into six subpopulations, including two relatively large subpopulations in the central and southeastern Koʻolau Mountains that contained over 400 birds each, a smaller subpopulation of about 25 birds in Waikane and Kahana valleys on the windward (eastern) side of the island, and three tiny remnants consisting of 1–4 birds in Nuʻuanu, Waiheʻe, and Waiahole valleys. Moanalua Valley had the most ʻelepaio territories (n = 79), but Wailupe Valley had the most breeding pairs (n = 51).

DISCUSSION

The current total population size of the Oʻahu ʻElepaio, obtained by combining the results of this study for the Koʻolau Mountains and those reported by VanderWerf et al. (2011a) for the Waiʻanae Mountains, is 1,261 birds (95% CI = 1,205–1,317), which consists of about 477 breeding pairs and 307 single males. This estimate is roughly 50% lower than the previous estimate of 1,974 birds that was based on surveys conducted in the 1990s (VanderWerf et al. 2001). Most of the decline has occurred in the Waiʻanae Mountains, where ʻelepaio numbers dropped from about 950 in the 1990s to only 300 in 2006–2009, though some of the decline was caused by overestimation in the 1990s (VanderWerf et al. 2011a). In contrast, the status of the Oʻahu ʻElepaio in the Koʻolau Mountains has remained more stable, with 1,020 birds estimated to occur in the 1990s and about 961 today.

The geographic range of the Oʻahu ʻElepaio has declined by about 75% over the past 40 years, from to 21,563 ha in 1975, to 5,483 ha in

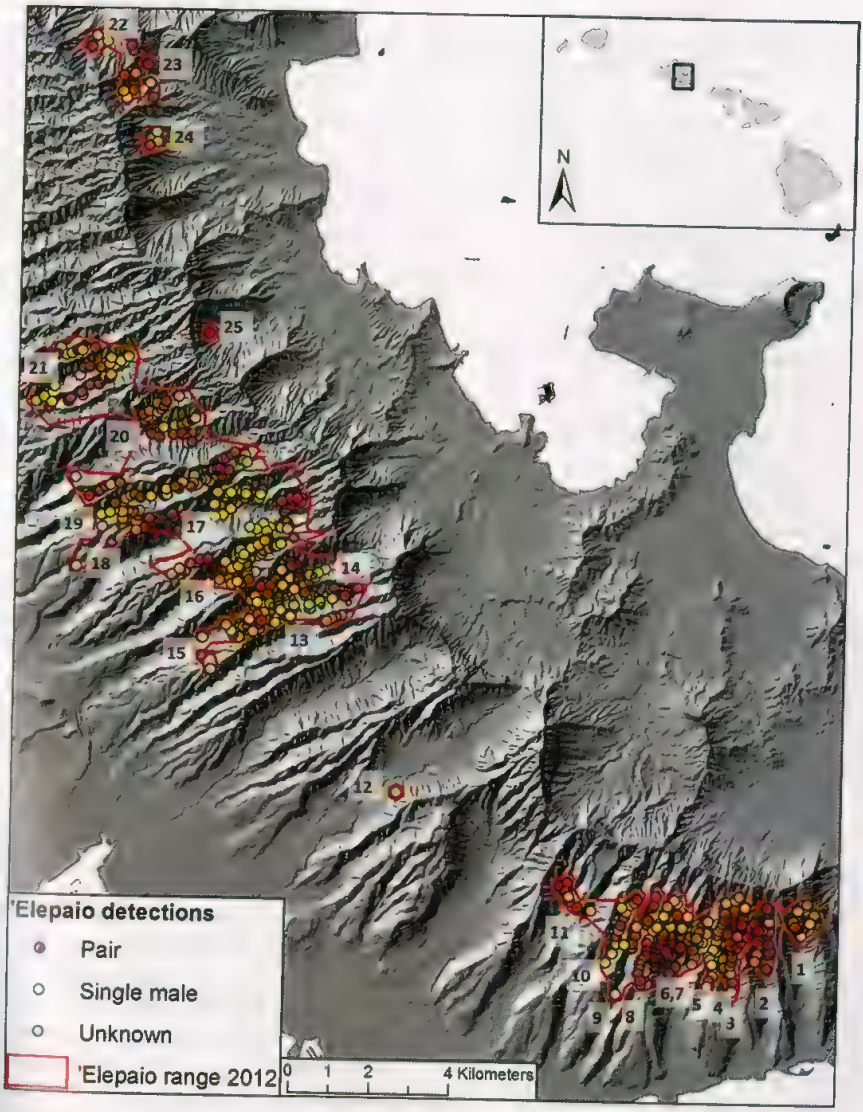

FIG. 1. Locations of detections of O'ahu 'Elepaio in the Ko'olau Mountains in 2011–2012. Numbers correspond to the Location Codes listed in Table 1.

1990s, and 5,187 ha in 2011–2012 (Table 2). The range is now highly fragmented, and most subpopulations are isolated from each other by unsuitable habitat and the limited dispersal behavior of 'elepaio (VanderWerf 2008). The pattern of decline in geographic range has varied among regions and among time periods. In the Ko'olau Mountains of eastern O'ahu, the range declined by 80% from 1975 to the 1990s, but since the 1990s rate of decline has slowed or even stopped in some areas. The range in the central Ko'olau Mountains appears to have increased since the 1990s (Table 2), but this was caused by more thorough survey coverage in 2011–2012 and the rediscovery of 'elepaio in two valleys where they were thought to have disappeared (Waimano, Waimalu). 'Elepaio have continued to decline on the windward side of the Ko'olau Mountains, in Waikane, Kahana, and Waiahole Valleys. In contrast, in the Wai'anae Mountains of western O'ahu, the range of 'elepaio declined by 50% from 1975 to the 1990s, and has continued to decline at the same rate. The only large subpopulations left in the Wai'anae range occur in areas

TABLE 1. Abundance of O'ahu 'Elepaio in the Ko'olau Mountains. Locations are listed from southeast to northwest in each region. Location codes correspond to numbers shown in Fig. 1.

Code	Location	# pairs	# single males	Proportion pairs
1	Kuli'ou'ou+Ka'alakei Valleys	8	5	0.62
2	Kupaua Valley	15	2	0.88
3	Pia Valley	32	7	0.82
4	Hawai'iloa Ridge	6	2	0.75
5	Kulu'i Valley	7	12	0.37
6	Wailupe Valley east fork	8	9	0.47
7	Wailupe Valley west fork	43	12	0.78
8	Wiliwilinui Ridge+Waialae Iki	10	7	0.59
9	Kapakahi Gulch	9	2	0.82
10	Waialae Nui Valley	4	9	0.31
11	Palolo Valley	5	2	0.71
	Southeastern Ko'olau Total	145	71	0.67
12	Nu'uanu Valley	0	1	0.00
13	Manaiki Valley+Tripler Ridge	2	3	0.40
14	Moanalua Valley upper	20	14	0.59
15	Moanalua Valley lower	18	27	0.40
16	South Halawa Valley	24	26	0.48
17	North Halawa Valley	26	25	0.51
18	Aiea Loop Trail	7	3	0.70
19	Kalauao Valley	30	22	0.58
20	Waimalu Valley	20	11	0.65
21	Waimano Valley	14	16	0.47
	Central Ko'olau Total	162	146	0.53
22	Kahana Valley	3	2	0.60
23	Waikane Valley	6	4	0.60
24	Waiahole Valley	1	3	0.25
25	Waihe'e Valley	1	0	1.00
	Windward total	11	9	0.55
	Grand Total	317	228	0.58

where the primary threat, nest predation by rats, has been managed (VanderWerf et al. 2011a, b).

The current surveys were more thorough than those in the 1990s and the population estimates were obtained by somewhat different methods, so care is needed in comparing the results and interpreting the apparent trends. During surveys in the 1990s, some areas were surveyed only partially and the density of territories was extrapolated to produce an estimate for a larger area. For example, in the 1990s only the lower section of Kalaua'o Valley was surveyed, which produced only a few 'elepaio, but the current surveys revealed that many more 'elepaio were present higher in the valley. Similarly, zero 'elepaio were detected in Waimano Valley in the 1990s when only the lower section was surveyed, but in the current surveys we detected 14 pairs and 16 single male elepaio in the higher portions of the valleys that were not surveyed previously. The number of 'elepaio estimated to occur in the central leeward Ko'olau Mountains thus appears to have increased from about 226 in the 1990s to over 500 today, but this difference is primarily because of greater survey effort.

Although we attempted to survey as much of the Ko'olau Mountains as possible, some areas were simply too steep to access on foot. A few 'elepaio probably occur in areas we did not survey, including the upper reaches and tributaries of some larger valleys, such as South Halawa and Waimalu, that were blocked by waterfalls and would have required rappelling from adjacent ridges in order to survey. Some areas that we did not survey in 2011–2012 have been surveyed repeatedly in the past and have yielded zero 'elepaio for many years, including the Kahuku Training Area, Schofield Barracks East Range, and other areas in the northern Ko'olau Mountains managed by the U.S Army (VanderWerf et al. 2001, OANRP 2012).

The primary management tool for the O'ahu 'Elepaio has been rat control to reduce nest

TABLE 2. Geographic range size (ha) of O'ahu 'Elepaio subpopulations in the Ko'olau and Wai'anae Mountains in 1975, the 1990s, and 2011–2012. Merged cells indicate subpopulations that formerly were continuous.

Mountain range	Subpopulation	1975	1990s	2011–2012
Ko'olau	Southeastern Ko'olau		1,063	
	Palolo		78	1,019
	Manoa	2,391	16	0
	Nu'uanu		Unknown	10
	Kapalama	414	0	0
	Central Ko'olau	11,059	1,396	2,724
	Maunawili	344	0	0
	Waihe'e		32	10
	Waiahole	1,255		30
	Waikane-Kahana		523	155
	Hau'ula	120	0	0
	Kahuku	121	0	0
	Ko'olau Total	15,705	3,120	3,948
Wai'anae	Palehua			121
	Palikea-Palawai			118
	Puali'i	1,732	1,165	9
	'Ekahanui-Kalua'a			308
	Lualualei			0
	Schofield West Range	783	532	364
	Makaha-Wai'anae Kai		459	230
	Makua		19	77
	Pahole-Kahanahaiki	3,343	0	134
	Ka'ala		21	12
	Wai'anae Total	5,857	2,363	1,239
Both	Grand Total	21,563	5,483	5,187

predation (VanderWerf 2009, VanderWerf et al. 2011a), and the beneficial effects of this technique on 'elepaio demography were evident during surveys. In areas where rats have been controlled, 'elepaio numbers have remained stable or increased and the proportion of pairs was higher. This pattern was most striking in Wailupe Valley, where rats have been controlled in the west fork but not in the east fork, and in Moanalua Valley, where rats are controlled only in the upper portion of the valley (Table 1). Areas where rats are controlled likely serve as sources of emigrants that help to support 'elepaio numbers in nearby areas, but predation by rats on nesting females causes the adjacent areas to act as sinks (VanderWerf 2009).

O'ahu 'Elepaio have declined severely on the windward (eastern) side of the Ko'olau Mountains, where estimated numbers dropped from 272 birds in the 1990s to only 35 today. Some of this decline may have been caused by an overestimate of the number of birds in Kahana Valley, which was only partially surveyed in the 1990s, but 'elepaio have disappeared from much of Waikane and Waiahole Valleys where they were known to occur previously. Rats were controlled in Waikane Valley for several years by the U.S. Army but the control effort was not sufficient and 'elepaio numbers continued to decline (VanderWerf et al. 2011a). Management of the remaining 'elepaio in Waikane should be resumed using new techniques, including native forest restoration, to prevent extirpation of 'elepaio from the windward side of the island. If active management is resumed in Waikane, translocating the few remaining 'elepaio from other valleys on the windward side to Waikane could be considered in order to consolidate the last remnants and provide a greater overall chance of persistence.

'Elepaio numbers have increased or remained stable in some areas where no rat control or other active management has been conducted, possibly because of changes in 'elepaio behavior and geographic variation in forest structure. VanderWerf (2012b) showed that 'elepaio in southeastern O'ahu are evolving to nest higher off the ground in response to predation by rats, and it is possible that the continued presence of 'elepaio in areas that receive no management is caused by similar changes in nesting behavior or by changes in habitat use. For example, 'elepaio numbers in

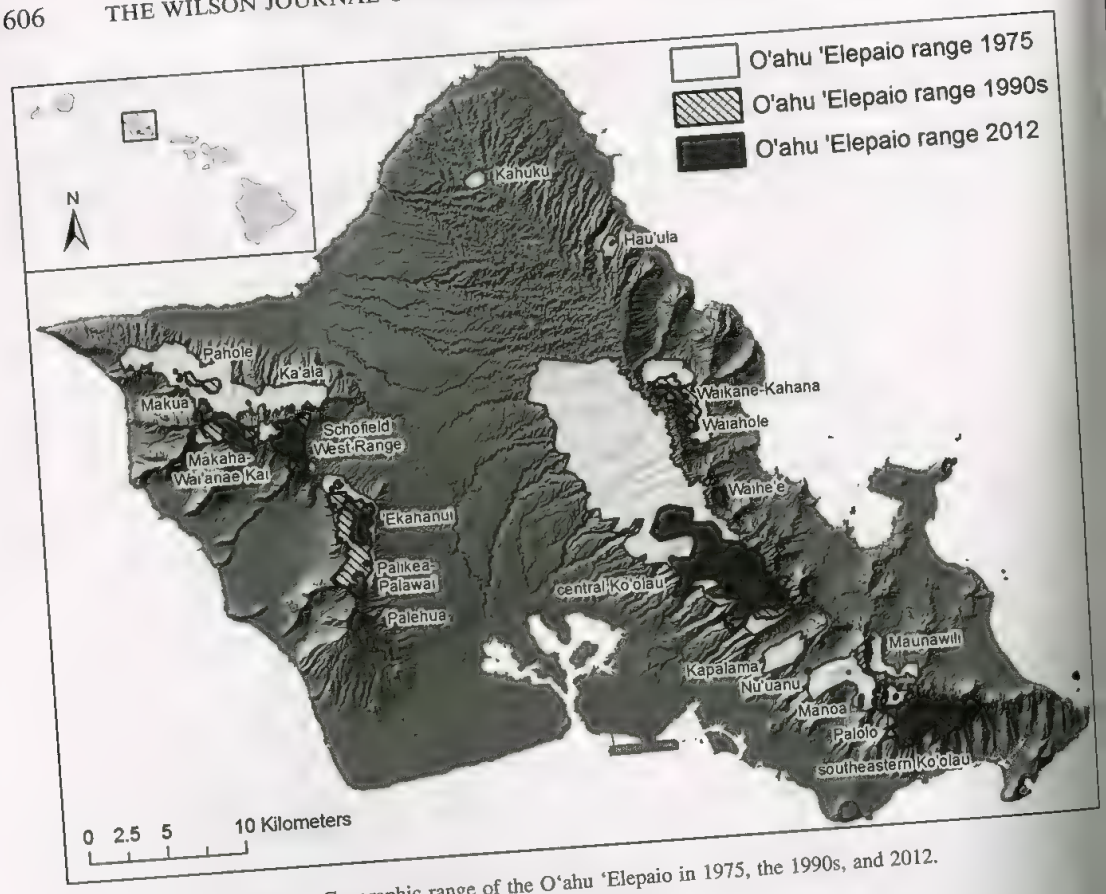

FIG. 2. Geographic range of the O'ahu 'Elepaio in 1975, the 1990s, and 2012.

'Aiea have increased from only one pair and one single male in the 1990s to seven pairs and three single males today. In 2011, we observed an 'elepaio pair in 'Aiea nesting in a *Eucalyptus robusta* tree over 30 m tall, where they likely were safe from rats. 'Elepaio have not been observed using this alien tree species previously, though it is common on O'ahu. If this behavior becomes widespread and more 'elepaio begin using tall alien trees that lack fruit they may suffer lower rates of nest predation. In Waialae Iki Valley, we found that 'elepaio were common in forest consisting almost entirely of 20-m tall strawberry guava trees with virtually no understory. In such habitat, 'elepaio have no choice but to nest high off the ground, where nest predation by rats is less likely. Forest structure, dynamics, and tree species composition all may play a role in determining whether 'elepaio can persist in an area. Kalaua'o Valley, which supports one of the densest concentrations of O'ahu 'Elepaio and contains relatively intact native forest in the upper reaches, has been proposed as a natural area reserve by the Hawai'i Division of Forestry and Wildlife. Such designation may result in more funding for management to prevent the spread of non-native trees and support the persistence of 'elepaio.

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FIRST BREEDING RECORDS OF NONGGANG BABBLER (*STACHYRIS NONGGANGENSIS*) IN A LIMESTONE AREA IN SOUTHERN CHINA

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ABSTRACT.—We present the first breeding records of Nonggang Babbler (*Stachyris nonggangensis*), a newly described bird species found in the limestone area of southwestern Guangxi, in southern China in 2008. The records presented here include information on behavior, nest, egg, incubation, and reproductive success rate. We discovered six nests (including three active nests) through systematic checking and radio tracking. Most Nonggang Babblers were found to begin foraging in pairs (male and female) from mid to late March. They build their nests in April. The nests were placed in cavities in a limestone cliff or on a massive rock located on the mountainside at altitudes ranging from 206–323 m. The nests were made of aerial roots, leaves, twigs, and soft grasses. Nonggang Babblers would lay 4–5 pure white eggs with an average fresh weight of 4.80 ± 0.11 g. Female Nonggang Babblers would spend 74.5 ± 5.0% of the day incubating their eggs, and the incubation period would last >18 days. We propose that Nonggang Babblers could prolong the incubation period and reduce foraging time to enhance the survival rate of fledglings. The high nest predation rate is an important limiting factor for the population growth of Nonggang Babblers. *Received 9 September 2012. Accepted 2 March 2013.*

Key words: breeding parameters, incubation rhythm, karst landform, life history, nest site selection, Nonggang Babbler, *Stachyris nonggangensi.*

The Nonggang Babbler (*Stachyris nonggangensis*), a medium-sized passerine with a body length of ~17 cm. It is a recently discovered species from the Sino-Vietnamese border region of China (Zhou and Jiang 2008). Because of the species' unique characteristics which differ from other members of the Timalidae, Nonggang Babbler is recognized as an endemic bird in the limestone area (Eames 2008, Yang and Lei 2009, Zheng 2011). Nonggang Babblers are restricted to the well-protected limestone forest and are only recorded in Longzhou and Jingxi counties in southwestern Guangxi (Shu et al. 2009, Zhou et al. 2011). The population size of Nonggang Babblers is currently estimated to be ~1,500 individuals (Li et al. 2013). Because of the species' small range and special habitat requirements, the Nonggang Babbler has been classified as vulnerable in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (BirdLife International 2012).

As the Nonggang Babbler is a recently described species, very little is known about the nest and breeding ecology. The breeding season has been assumed to begin in late February (Zhou and Jiang 2008). However, the breeding ecology of *Stachyris* birds and other babblers that inhabit the limestone forest has not yet been fully described (Collar and Robson 2007). Therefore, to understand the breeding ecology of Nonggang Babblers, we conducted a field study at the Nonggang National Nature Reserve (NNR) in southwestern Guangxi from 2009 to 2012. In this study, we describe the behavior, habitat, nest, eggs, and incubation period of Nonggang Babblers.

METHODS

Study Area.—This study was conducted from April 2009–August 2012 in a limestone forest at Nonggang NNR, southwestern Guangxi Zhuang Autonomous Region, in southern China. Nonggang NNR (22° 28′ N, 106° 57′ E), approximately 10,077 hm^2 in area, is a typical karst landscape with abundant limestone outcrops and depressions at an altitude that ranges from 150–650 m. Natural vegetation, mainly dominated by limestone hill seasonal rainforest, covers 98% of the nature reserve. The forest on the hillsides is composed of calciphiles such as *Burretiodendron hsienmu* and *Cephalomappa sinensis*. *Monocladus amplexicaulis* and some shrubs mostly occupy the peaks with less water and soil (Shu et al. 1988). Nonggang NNR is located in the northern margin of the tropics with a mean annual temperature ranging from 20.8–22.4 °C and a mean annual rainfall ranging from 1,150–1,550 mm. Rain

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TABLE 1. In 2011–2012, we captured five Nonggang Babblers, weighed them, withdrew blood for sex determination, and fitted them with radio transmitters to learn more about this little-known species. Out of five nests for these individuals, likely only one was successful.

No.	Year	Frequency (Hz)	Capture date	Stop date	Sex	Body weight (g)	Breeding result
1	2011	151.183	March 8	April 2	♂	36.2	Unknown
2	2011	151.149	March 12	June 22	♂	37.8	Succeeded
3	2011	151.138	March 30	June 22	♀	37.0	Nest Predated
4	2012	151.443	March 13	April 15	♂	38.3	Unknown
5	2012	151.100	March 20	May 21	♂	37.0	Unknown

comes seasonally, and approximately 76% of rainfall precipitates between May and September (Nong 1988).

Surveys for Nonggang Babblers.—Field surveys were conducted in the following periods: April 2009, April–May 2010, January–July 2011, and March–August 2012. Systematic checks of rocks and other possible habitats were conducted daily to search for nests. Although Nonggang Babblers are common in winter, we did not find any active nests in 2009 and 2010. In 2011 and 2012, we used Biotrack PicoPip transmitters coupled with AG392 batteries to help search for nests. We captured Nonggang Babblers using playback and mist nets. When we captured a babbler, we would measure its body mass and collect approximately 1 ml of blood in order to determine its sex. Whenever a pair of Nonggang Babblers was captured, only one would be fitted with a transmitter. The other would be banded with a colored ring on the tarsus. Five transmitters that weighed 1.10 g (Table 1), including the Teflon harness, and averaged 3.0% of the body mass were fitted using backpacks (Rappole and Tipton 1991). We tracked the babblers on foot using a handheld six-element Yagi antenna and receiver. As the Nonggang Babbler is an audacious bird, we could easily follow and observe it from dawn to dusk in the limestone area. We recorded the daily behavior that included calls, courtship, foraging, resting, and collecting nest materials. Three researchers and one field assistant took about 300 days to search for nests and observe behaviors in this study.

Upon finding a nest, we would record its altitude, shape, and dimensions (i.e., diameter, height, and depth). The nests of the Nonggang Babblers were always located in a cavity of a large rock. Therefore, we also measured the characteristics of the cavity, including the height above ground, direction, length, width, and depth. We also estimated the density and coverage of trees (diameter at breast height >10 cm) or shrubs in a 10 m × 10 m quadrant, with the nest at its center. When a Nonggang Babbler would leave its nest, we would analyze the nest's material components.

After a Nonggang Babbler laid its last egg, we measured the fresh weight, length, and width of the eggs. We also used a data logger (ZDR-21, China Hangzhou Zeda Instruments Co., Ltd.) to help monitor the daily nest attendance. This data logger has two thermocouples. One was inserted into the nest close to the eggs; whereas, the other was placed outside the nest to measure the ambient air temperature. The data logger was set to record the temperature every 90 secs. The sex of the Nonggang Babblers was identified using the CHD gene which is carried on the avian sex chromosomes (Griffiths et al. 1996). We used PCR primers P8/P2 and 2550F/2718R to amplify the CHD genes (Griffiths et al. 1998, Fridolfsson and Ellegren 1999). Details of the molecular work and sexing characteristics are based on a previous study (Dubiec and Zagalska-Neubauer 2006).

RESULTS

Behavior.—Based on five birds tracked throughout the day and some directly observed individuals, Nonggang Babblers foraged in single-species flocks with 11.6 ± 2.2 (n = 36, range 8–15) individuals from late August to late February or early March of the following year. Occasionally, they were seen in mixed-species flocks led by Grey-cheeked Fulvettas (*Alcippe morrisonia*). Most Nonggang Babblers were observed foraging in pairs from mid to late March. Apparently, Nonggang Babblers find their partners when foraging in flocks. They usually begin their day at 0600 to 0700 hrs and end at 1700 to 1830 hrs during March and May. They roost in the bushy

shrubs located in the limestone peak at night. At noon, however, they would usually rest on a horizontal branch or vine. In the 44 observations, we observed males and females preen singly 32 times and preen each other 12 times before the females laid eggs. Because we have not observed copulation, we predict that preening may be an important courting behavior of Nonggang Babblers and used to maintain family relationships.

Nest Construction.—We first observed a pair of Nonggang Babblers collect nest materials on 1 April 2011. They also searched at least six limestone cavities, four of which were left with a few leaves for the nest. They started to build the final nest on 9 April and finished on 12 April. Another pair began to build their nest on 24 April 2011. Based on our observations, females mostly chose the nest hole. We saw the female of a pair enter into the hole before the male six times. If the hole was suitable to build the nest, the male would usually give the female leaves or twigs to lay the foundation. Then, both the male and female of the pair constructed the nest.

Only three active nests were observed in our field survey from 2009–2012. The nests appeared as open bowls with irregular edges (outer diameter: 15.3 ± 1.8 cm, inner diameter: 7.7 ± 0.3 cm, outer nest height: 11.67 ± 2.52 cm, bowl depth: 5.50 ± 0.50 cm, $n = 3$) and were mostly made of materials collected from around the nest sites (Fig. 1a, c). The innermost lining of the three nests were all made of aerial roots of *Tetrastigma* sp. and soft grasses. The outer layers of the nests were made up of dry leaves and twigs of *Excetrodendron hsiemvu*, *Cephalomappa sinensis*, and *Hydnocarpus hainanensi*. Another nest near the peak was mostly made up of dry bamboo leaves (*Monocladus amplexicaulis*) (Table 2).

Nest Site Characteristics.—Six nests of Nonggang Babblers, including the three nests that were initially built but were not used, were placed in cavities of a limestone cliff or a big rock located on the mountainside with an altitude ranging from 206–323 m (Fig. 1b, Table 3). The mean height of the nests above ground was 5.4 ± 4.3 m. Most of the cavities supporting the nests faced the northwest side and had a height of 50.1 ± 4.3 cm, width of 22.8 ± 5.6 cm, and a depth of 38.4 ± 14.5 cm. The occupied nests were located in the limestone forest with more big rocks. The density of all tree species (DBH > 10 cm) and the shrub density were 6.3 ± 4.8/100 m^2 and approximately 4.7 ± 2.4/m^2, respectively. Human disturbance may be an important factor in nest selection of Nonggang Babblers. The distances of the nests from the path and the forest edge were 57.7 ± 24.0 m and 509.0 ± 136.2 m, respectively. However, Streaked Wren-Babblers (*Napothera brevicaudata*), another bird species associated with limestone, would also build nests in cavities of big rocks. They built their nests approximately 4.5 m away from the nest of Nonggang Babblers.

Eggs.—The eggs in two nests were observed during the 4-year field study. After the nest was built, a period of approximately 7 days was observed before the first egg was laid. One couple tracked by a transmitter finished its nest on 12 April 2011. The first egg was laid on April 19 between 0530 and 0700 hrs. The first four eggs were laid on successive mornings; however, the fifth egg was laid on the sixth day. The eggs of Nonggang Babblers were pure white and had no spots (Fig. 1a, c). The fresh weight of eight eggs was 4.80 ± 0.11 g (4.70–5.00 g), or approximately 13.0% of the body weight of an adult Nonggang Babbler (Table 4). The dimensions of the eight eggs from the two nests were 24.99 ± 0.37 mm (24.57–25.64 mm) in length, 18.88 ± 0.24 mm (18.62–19.20 mm) in breadth, and 8,910.47 ± 285.75 mm^3 (8,518.53–9,289.73 mm^3) in egg volume index (length × $width^2$). The clutch sizes of the Nonggang Babblers were 4–5 eggs.

Incubation and Incubation Rhythm.—For the two breeding Nonggang Babblers we tracked by transmitters, one female bird was observed to incubate the eggs in the nest while the male foraged alone approximately 200 m away. A male which we tracked during the entire incubation period, copulated successfully with its mate, but he was never seen in the nest. Therefore, we believe that incubation of Nonggang Babblers is carried out solely by the females. Females usually began incubating after laying the last egg. After the 18-day incubation period, both of the nests were preyed upon and the broken eggs were abandoned. At that time, we observed that the embryos had begun to develop. Hence, we believe that the incubation period of Nonggang Babblers takes more than 18 days.

Based on female attendance and absence data for 18 days and about 18,000 temperature records, it seems the females establish a consistent incubation pattern. The females spent 74.5 ± 5.0% (range: 66.4–82.8%) of the day incubating

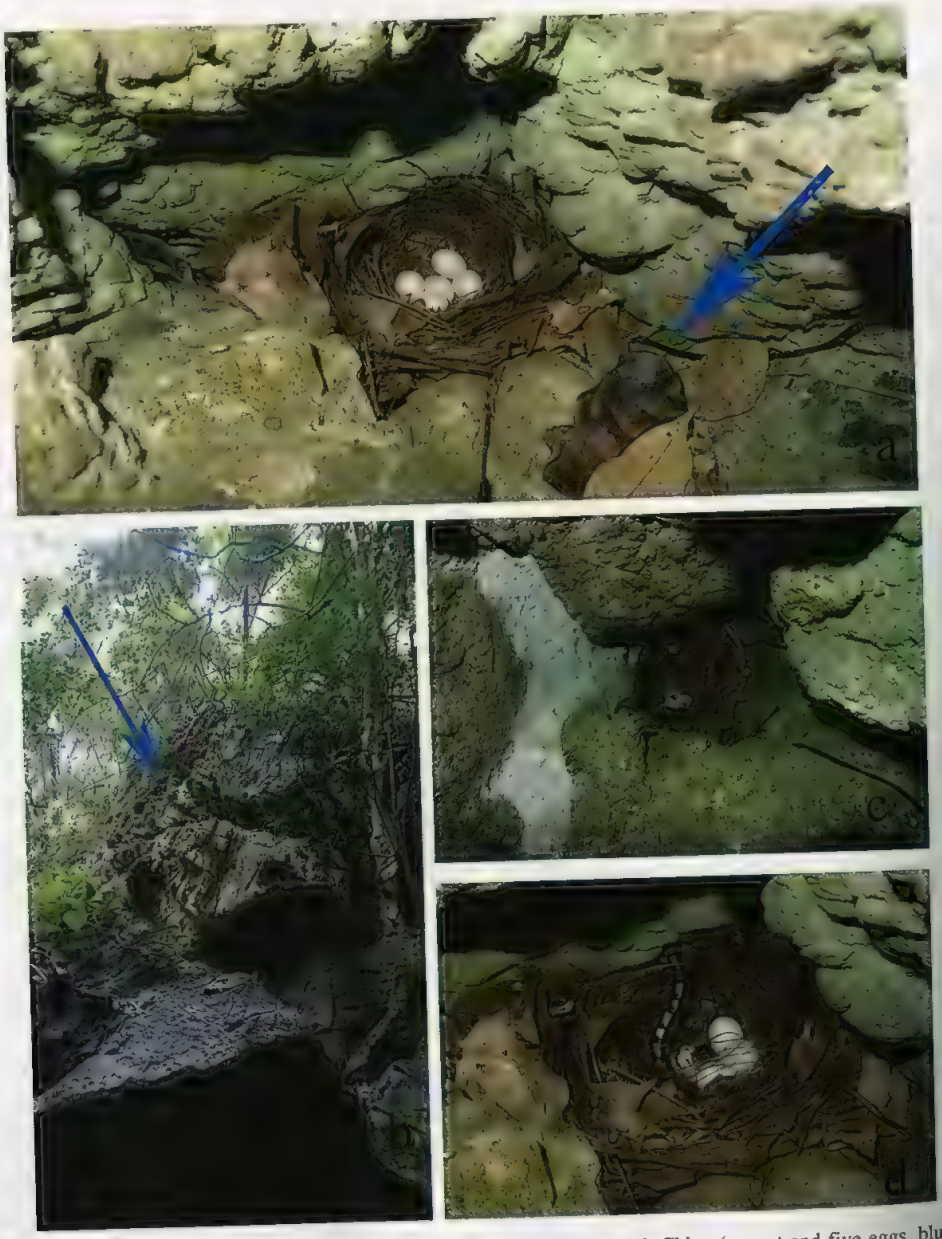

FIG. 1. The nest and eggs of Nonggang Babbler at Nonggang NNR, south China (a: nest and five eggs, blue arrow indicates the line of the Data logger. b: nest site, blue arrow indicates the hole which Nonggang Babbler put its nest. c. another nest with four eggs. d: nest predation by *Scolopendra subspinipes*).

the eggs and left the nest 2.22 ± 0.73 (range from 1–3) times per day to forage. However, females would spend more time in their nest as the incubation proceeded ($r = 0.59$, $P = 0.01$). The nest was well insulated, with an average temperature of 29.4 ± 1.5 °C during incubation and 21.3 ± 1.2 °C during the recess period.

Nest Predation.—Among the three nests we observed, there were no fledglings. The two nests observed in 2011 were possibly destroyed by *Scolopendra subspinipes* (Fig. 1d) and a leopard cat (*Prionailurus bengalensis*). The nest discovered in 2012 was possibly depredated by a snake. Although we could not find the nest of another

TABLE 2. Nest weight and percentage of materials used to support nests of Nonggang Babblers.

Nest No.	Nest weight (g)	Nest materials (%)				
		Dry twigs	Leaves	Bamboo leaves	Aerial roots	Canes
1	51.9	45 (17.7)	182 (71.7)		24 (9.4)	3 (1.2)
2	55.0	25 (8.7)	190 (66.0)		71 (24.6)	2 (0.7)
3	26.1	19 (15.7)	20 (9.2)	55 (25.3)	121 (55.8)	2 (0.9)

male babbler (continuously tracked by a transmitter until the end of breeding season), it was found foraging with a chick on a big limestone rock on 24 May 2011. Therefore, the nest predation rate of Nonggang Babblers was assumed to be approximately 75%.

DISCUSSION

Our discovery of six nests of Nonggang Babblers was the first breeding record for this newly described bird species from the limestone area in the Sino-Vietnamese border region. The Nonggang Babbler is considered an endemic in a well-protected limestone forest (Zhou and Jiang 2008, Shu et al. 2009). We found that Nonggang Babblers nest in cavities of large rocks located in the limestone forest with more rocks and fewer trees and shrubs. Nonggang Babblers may be considered limestone-dwelling birds, and their speciation and evolution are associated with the type of karst landform. After reports about Nonggang Babblers had been published, additional surveys for Nonggang Babblers were conducted in the limestone area of the southwestern Guangxi and southeastern Yunnan province. The species was discovered in a new site near Longzhou county (Zhou et al. 2011). Although limestone is a very common landform, well-developed karst landform and well-protected forests are very rare in the Sino-Vietnamese region. To assess accurately the status of Nonggang Babblers, conducting a suitable habitat and population survey in the limestone area is necessary.

When the Nonggang Babbler begins to incubate its eggs, it adopts a strategy of reducing recess period frequency and prolonging recess period duration. Nonggang Babblers usually leave their nest to search for food approximately 2–3 times a day, which is similar to some non-passerine birds (Hohman 1986, Sun et al. 2005). However, the behavior of Nonggang Babblers during incubation is similar to that of most passerine birds (Zerba and Morton 1983, Jiang et al. 2003). Normally, the incubation behavior is affected by environ-

TABLE 3. Nest site selection parameters of Nonggang Babblers.

Nest site parameters	Used and laid eggs in			Only placed materials		
	1	2	3	4	5	6
Year	2011	2011	2012	2011	2011	2011
Altitude (m)	323	216	234	229	215	206
Slope aspect	220	285	120	320	308	315
Slope	70	90	65	90	85	90
Nest height above ground (m)	4.5	8.3	1.7	1.1	12.5	4.4
Cavity orientation	310	265	203	325	—*	315
Cavity height (cm)	133.0	40.4	13.1	35.0	—	29.1
Cavity width (cm)	25.0	30.2	24.2	16.2	—	18.4
Cavity depth (cm)	26.0	30.1	27.4	53.4	—	55.0
Coverage above nest (10 cm × 10 cm)	100	100	100	100	—	100
Coverage above nest (50 cm × 50 cm)	95	100	98	100	—	100
Coverage above nest (1 m × 1 m)	95	95	95	95	—	100
Coverage above nest (10 m × 10 m)	90	85	80	95	90	95
Tree (DBH > 10 cm) density (/100 m^2)	8	11	5	12	1	1
Shrub density (/m^2)	3.2	6.6	6.2	7.2	3.6	1.2
Distance from path (m)	15	52	80	80	63	56
Distance from forest edge (m)	267	578	425	607	594	583

* The cavity was too high to be measured safely during the course of this study.

TABLE 4. Egg measurement of Nonggang Babblers in 2011 and 2012.

No.	Weight (g)	Length (mm)	Breadth (mm)	Volume index (mm^3)
1	4.88	25.00	19.20	9,216.00
2	4.84	25.30	19.00	9,133.30
3	4.70	24.60	18.90	8,787.37
4	4.71	24.80	18.80	8,765.31
5	5.00	25.20	19.20	9,289.73
6	4.70	24.57	18.62	8,518.53
7	4.70	24.80	18.63	8,607.51
8	4.90	25.64	18.70	8,966.05
Average	4.80 ± 0.11	24.99 ± 0.37	18.88 ± 0.24	8,910.47 ± 285.75

mental factors and body size (Afton 1980). Because of Nonggang Babblers' single-sex incubation pattern, the females must resolve the trade-offs in time allocated between keeping egg temperature adequate and foraging (Jia et al. 2010). Small-sized birds spend more time searching for food; hence, they spend less time in their nests during incubation. However, nest predation risk increases during the times that the female leaves her nest. If the female leaves for a prolonged period, the temperature of the eggs would decrease, which would then lead to incubation failure. A nest nest with good heat insulation could allow the female to leave her nest for a longer time and reduce the chance of nest predation. The incubation rhythm of Nonggang Babblers appears to compromise the conditions between egg cooling and nest predation. In addition, they have a longer incubation period (more than 18 days), which is rare in passerine birds. As Nonggang Babblers nest on rocks, their fledglings may be easily preyed on by a predator. Therefore, we hypothesize Nonggang Babblers tend to prolong their incubation period and reduce the nestling period to enhance the survival rate of the fledglings.

The nest predation rate of Nonggang Babblers is very high and similar to other tropical forest birds (Stutchbury and Morton 2001). The three observed nests were destroyed likely by a snake, a small carnivore, and *Scolopendra*, respectively. *Scolopendra* is a centipede commonly found in Nonggang NNR. Its body size measures approximately 20 cm in length. As a bird egg predator, it has not yet been fully described; however, we observed that it bit one egg of a Nonggang Babbler. We may suppose that nests on the ground or in rocks are easily preyed on by *Scolopendra* and may be a common incident in the tropical limestone forest.

The nests of Nonggang Babblers are usually located on a steep and high rock or cliff; thus, finding a nest through a systematic search for potential habitats is very challenging. Most researchers also encounter difficulty in reaching the nests because of their dangerous location; however, invertebrates, snakes, and other predators can easily locate them. The population distribution and growth rates are low in Nonggang NNR. We predict that a high nest predation rate is an important limiting factor for the population growth of Nonggang Babblers.

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FRUGIVORY BY TOCO TOUCAN (*RAMPHASTOS TOCO*) INHABITING A MOUNTAIN CHAIN IN THE BRAZILIAN CERRADO

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ABSTRACT.—I describe the feeding habits of *Ramphastos toco* (Toco Toucan) in relation to fruit abundance and diversity in a variety of habitat types in central Brazil. I traversed transects to sample fruit production and toucans that were feeding in four habitat types: two wet (streams and river) and two dry (cerrado and deciduous forest). Fruit abundance exhibited substantial temporal and spatial variability in which dry habitats provided fruits to toucans mainly in the dry season; the same occurred in the wet habitats during the rainy season. As a result, toucans experienced similar fruit diversity between seasons, while feeding niche breadth exhibited high values all year. The variable spatial and temporal fruiting patterns reflected differences among the vegetation of the four habitat types, and floristic variations between related sites as well. The data emphasize the importance of the peculiarities of a given site within a habitat mosaic and which should be included in conservation plans for declining species. *Received 3 September 2012. Accepted 12 January 2013.*

Key words: cerrado, feeding ecology, habitat mosaic, phenology, Ramphastidae.

In the Neotropics, the abundance and diversity of fruits are associated with a diverse fauna which relies on fruits as a food resource (Orians 1969, Karr 1976, Moegenburg and Levey 2003). Frugivorous vertebrates are the dominant group in the Neotropical forests and, in some areas, comprise much of the mammalian and avian biomass (Fleming et al. 1987, Terborgh et al. 1990). For these vertebrates, the diversity of fruiting species at a given site could be an important factor driving their foraging efforts (van Schaik et al. 1993, Kinnaird et al. 1996, Moegenburg and Levey 2003). Studies focusing on the responses of frugivores to extensive habitat heterogeneity have found overlapping patterns of fruit and frugivore abundance as result of a frugivore's ability to track fruit resources on a diversity of scales (Kinnaird et al. 1996, Moegenburg and Levey 2003, Tellería et al. 2005, Hampe 2008). Highly mobile frugivores such as birds tend to exhibit pronounced variation in local abundance according to the dynamics of fruiting patches (Powell and Bjork 1995; Kinnaird et al. 1996; Holbrook et al. 2002; Ragusa-Netto 2007, 2008a, b, 2010). However, in some cases the relationships between fruit production and frugivorous bird abundance were unclear, possibly as the result of the spatio-temporal scale and ecological context in which these interactions were focused (Herrera 1998, Tellería and Pérez-Tris 2007, Brown and Long 2006).

The interactions between fruits and frugivorous birds may influence the dynamics and distribution of bird and plant populations. The foraging behavior of frugivores helps shape plant distribution patterns, which result from differences in plant recruitment based on seed deposition patterns (Herrera 1988). Thus, the identification of important plant food resources for a particular bird species may be important in assessing its feeding habits and ecological role in the community (Kinnaird et al. 1996, Holbrook and Loiselle 2009). This could be useful in designing conservation areas to preserve the frugivores important for ecosystem regeneration (Holbrook and Loiselle 2009).

Toucans are prominent members of avian communities in Neotropical ecosystems (Terborgh et al. 1990). They often move considerable distances while feeding (Graham 2001, Holbrook 2011) and deposit intact seeds which assist in tree species regeneration (Howe 1981, Holbrook and Loiselle 2009). They may fly across fragmented forests (Graham 2001), enhancing gene flow across forest remnants and increasing plant diversity (Hamilton 1999). Therefore, a decrease in toucan populations may impede the regeneration of Neotropical forest areas (Holbrook and Loiselle 2009). Toco Toucans (*Ramphastos toco*: Short and Horne 2002) require a variety of habitat types, which provide food throughout the year (Saunders et al. 1991). Despite their persistence in fragmented forests, Toco Toucans suffer continued habitat loss because of the accelerated clearing of cerrado areas (Ratter et al. 1997, Short and Horne 2002, Carvalho et al. 2009; JRN, pers. obs.). In this study, I assessed the temporal and spatial variability in food resource abundance for Toco Toucans in a variety of habitat types in

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central Brazil, evaluated the relationship of the diet of Toco Toucans to food resource availability, and I analyzed the association between fruit species and habitat types used by Toco Toucans.

METHODS

Study Site.—Data collection was carried out near the city of Rochedo in the Maracaju mountain chain, Mato Grosso do Sul State (19° 54′ S, 55° 01′ W), in central Brazil. The study site has a dry tropical climate with a marked seasonality in precipitation, with 75% of the 1,400 mm average annual rainfall occurring from October–March, and a prolonged drought from April–late September. The area has a hilly topography varying in elevation from 400–900 m asl. The dominant vegetation type is dense cerrado (Brazilian savanna) on flat areas, deciduous forests on slopes, and semi-deciduous forests alongside the major water course (Aquidauna River), and permanent green gallery forest along streams.

Fruit Production.—To sample fruit production through habitat types (Bullock and Solis-Magallenes 1990, Chapman et al. 1994), I established 12 phenology transects of 300 m × 4 m, with three transects in each of four habitat types: (1) deciduous forest, (2) dense cerrado, (3) large (Aquidauna River), and (4) small watercourses. Transects in deciduous forest were positioned in three foothill areas of the Maracaju cliffs (mountain chain: 19° 53′ S, 55° 00′ W; 19° 54′ S, 54° 59′ W; 19° 54′ S, 55° 05′ W). The same was done in the dense cerrado (19° 55′ S, 54° 56′ W; 19° 56′ S, 55° 01′ W; 19° 57′ S, 54° 54′ W), so that transects were at least 2,000 m apart one from each other. The transects along the Aquidauna River were in three segments of riparian forest (at least 1,000 m apart; 20° 00′ S, 54° 53′ W; 20° 01′ S, 54° 55′ W; 20° 03′ S, 54° 55′ W). I positioned one transect in the gallery forest of each stream (at least 2,000 m apart from another stream: carrapato: 19° 56′ S, 54° 56′ W; onça: 19° 51′ S, 54° 57′ W; and lageado, 19° 58′ S, 54° 52′ W).

Transects were monitored during the third week of each month from January–December 2008. I checked individual crowns for the presence of fruits with 8 × 40 binoculars. Fruit bearing trees greater than 15 cm diameter at breast height (dbh) were recorded when detected within a 2-m band on either side of the transect line. Where a tree occurred on the boundary of the 2-m transect, the tree was included if the mid-point of the trunk was rooted within the transect area (Renton 2001). I ranked the abundance of fruits at a given crown on a relative scale, ranging from total absence (0) to a plentiful fruit crop (4; Fournier 1974). Thus, for each habitat type, the sum of scores resulted in a monthly index of fruit abundance. Tree species were identified by comparison with samples in the herbarium at the Universidade Federal do Mato Grosso do Sul (Campus Três Lagoas); nomenclature followed Lorenzi (1994, 1998).

Food Resources of the Toco Toucan.—The diet of *Ramphastos* toucans consists mostly of canopy fruits (Sick 1997; Galetti et al. 2000; Short and Horne 2002; Ragusa-Netto 2006, 2008a, 2010). Toco Toucans are highly frugivorous (Ragusa-Netto 2006, 2008a, 2010) and inhabit marked seasonal areas (Sick 1997, Short and Horne 2002). To sample the feeding habits of Toco Toucans, I used the permanent access trails along which I positioned the phenology transects. Every month, I walked those trails for 32 hrs (8 hrs/habitat type), from 0600 to 1100 hrs, and again from 1500 to 1800 hrs, in the dry season; 0500 to 1000 hrs, and from 1600 to 1900 hrs (real time), in the wet season. These corresponded to peak activity periods for the Toco Toucans (Marsden 1999). Toucans may spend prolonged periods (up to 10 mins; Howe 1981) foraging in a given tree crown. To avoid resampling toucans feeding on a specific food source during an observation period, I walked the trails only in one direction. Whenever I spotted at least one foraging toucan, I recorded: a) tree species, b) food resources (flower, fruit, or animal prey), c) part eaten (petal, nectar, pulp, or aril), and d) number of toucans eating. If toucans captured animal prey, I recorded the size (cm, visually estimated) and taxa (usually the order). I recorded only the first ingestion of a specific food item eaten by Toco Toucans. I used only the initial, instead of sequential observations of feeding toucans, to assure the independence among feeding samples (Hejl et al. 1990).

Data Analyses.—In seasonal forests, fruiting patterns fluctuate exhibiting short periods of pronounced fruit enhancement followed by abrupt declines (Justiniano and Fredericksen 2000, Funch et al. 2002, Ragusa-Netto 2008b). Hence, in the course of a season, variations in fruit production have implications for frugivores (van Schaik et al. 1993). Taking into account the potential intra-seasonal changes in fruit production, at each habitat type (Renton 2001; Ragusa-

Netto 2007, 2008a, 2010), I grouped fruit production into four periods of the year: the late wet season (Jan–Mar), the early dry season (Apr–Jun), the late dry season (Jul–Sept), and the early wet season (Oct–Dec). In each period, I analyzed the following parameters: a) feeding activity of Toco Toucans, b) fruit diversity, and c) niche breadth value. For every period, the accumulated monthly index of resource abundance (=sum of scores) was taken as a variable for analyses. I compared fruit production between habitat types across seasons with a two-way analysis of variance (ANOVA). The first fixed factor had four levels: habitat types (cerrado, dry forest, river, and streams) and a second fixed factor: the four periods of the year (Jan–Mar, Apr–Jun, Jul–Sept, and Oct–Dec). The score data were log transformed to achieve normality and reduce heteroscedasticity (Shapiro-Wilk test, $W = 0.987$, $P = 0.471$. As Toco Toucans were not individually marked, I used the feeding records to avoid pseudoreplication. This data consisted of the number of times a given food item was consumed, regardless of the number of feeding toucans, time they spent feeding, and amount of food ingested. I used feeding records to calculate the distribution of food species consumed by Toco Toucans (Table 1). For the analysis of the extent of food resources used, I counted the number of toucans feeding together with the proportion of every food item used by them (Table 1). I evaluated the range of their diet by analyzing niche breath, using the standardized Hurlbert's niche breadth index, because it incorporates a measure of the proportional abundance of resources used (Hurlbert 1978). To calculate this parameter, I used the sum of scores of fruiting trees exploited by Toco Toucans, as well as the proportion of feeding records on a particular food item. A value close to 0 indicates dietary specialization, and a value close to 1 indicates a broad diet (Hurlbert 1978). I used the Simpson index (D) (Simpson 1949) to describe the fruit diversity available to Toco Toucans. The Simpson index is sensitive to changes in common species. Because Toco Toucans are generalist frugivores (Ragusa-Netto 2006, 2008a, 2010), I chose the Simpson index to minimize the influence of fruit diversity indices of the rarely available fruits and to emphasize changes in the commonly available ones. To compare fruit diversity in the four periods of the year, I used a Chi-square test. To analyze the Toco Toucan's temporal use of feeding areas, I used Chi-square contingency analysis to test for differences in the number of feeding records in each of the four habitat types in the four periods of the year. To improve the evaluation on the temporal use of feeding areas according to fruiting species, which bore fruits simultaneously in more than one habitat type, I conducted a correspondence analysis (CA) to explore the variation in the use of feeding areas associated to the common fruit species (>2.5% feeding records, Table 1). Correspondence analysis is an ordination method adequate for comparing associations containing counts of taxa, or counted taxa across associations. Like other ordination methods, CA attempts to place similar samples in similar positions in the ordination plot. The measure of distance between samples is proportional to the Chi-square statistic. Samples considered for this ordination procedure consisted of the number of feeding records for Toco Toucans at each habitat type (rows) on every fruit species (columns). Only food-plant species for Toco Toucans (Table 1), and respective fruit abundance (=sum of scores), were included in the above analyses.

RESULTS

Fruit Production.—In the phenology transects, I recorded a total of 16 fruit species of 11 families exploited by toucans (Table 1). Three species belonged to Leguminosae, two to Dilleneaceae, and two to Rubiaceae. The other families each had only one species (Table 1). At every habitat type, fruiting patterns exhibited highs and lows, so that the four habitat types exhibited no difference in general fruit production ($F = 1.87$, $P = 0.16$). However, fruit abundance differed significantly according to year period ($F = 3.34$, $P = 0.031$). There was a significant interaction between the two main factors (habitat type and year period; $F = 2.75$, $P = 0.017$), because of major fruit production either in dry areas (cerrado + dry forest) in the late dry season, or wet ones (streams + river) in the early rains (Figs. 1, 2). At streams, fruit production was prominent in the wet season, while in the early dry season fruit production declined with the lowest values found in May (Fig. 2A). At rivers, resource abundance increased in February, April, and May. From June to September, fruit production declined up to the beginning of the rainy season in October (Fig. 2B). The deciduous forest exhibited a fruiting peak from the middle to the late dry

TABLE 1. Plant species, percentage of feeding records (n = 271), and the number of Toco Toucans (*Ramphastos toco*) recorded feeding in each habitat type in the Maracaju mountain chain (Rochedo, State of Mato Grosso do Sul, Brazil, 2008).

Plant taxa	Feeding records (%)	N° of feeding toucans	Item	Months	Habitat type
Annonaceae					
Xylopia aromatica	3.4	13	Aril	November, December	Stream, Cerrado
Araliaceae					
Schefflera morototoni	22.8	89	Pulp	May, June, July, August, September, October	Forest, Cerrado, Stream
Cecropiaceae					
Cecropia pachystachya	21.9	92	Pulp	All year	Stream, River
Dilleneaceae					
Curatella americana	2.9	11	Aril	October, November	Cerrado
Davilla elliptica	0.7	3	Aril	September	Cerrado
Lauraceae					
Nectandra cissiflora	13.5	50	Pulp	October, November, December	Stream, Forest, River
Leguminosae					
Copaifera langsdorffii	15.7	62	Aril	May, June, July, August, September	Cerrado, Forest, River
Guibourtia hymenaefolia	1.9	7	Aril	April, May	Forest
Inga sp.	1.5	6	Aril	May, November	River, Stream
Meliaceae					
Guarea guidonea	2.9	8	Aril	October, November, December, January	River, Stream
Guarea kuntiana	0.7	4	Aril	June, July, August	Stream
Moraceae					
Ficus calyptroceras	1.1	6	Pulp	March, April	Forest
Myrtaceae					
Myrcia bella	3.3	12	Pulp	January	Cerrado
Rubiaceae					
Genipa americana	1.5	5	Pulp	August, September, October	River, Stream
Rudgea virbunoides	2.6	9	Pulp	February	Cerrado
Sterculiaceae					
Sterculia striata	0.7	3	Aril	October	Forest
Caterpillar	1.8	5		October, November	Cerrado
Eggs	1.1	2		October, December	River, Stream
Total	100	387			

season (Fig. 2C). In the rest of the year, few species and trees fruited in this area. In the cerrado, a minor peak in resource abundance occurred from the middle to end of the wet season. Then, fruit production declined to the lowest level in May. From the middle to the end of the dry season, fruiting in the cerrado was prominent (Fig. 2D).

Fruit diversity available to toucans fluctuated moderately during the year (Fig. 3A). Equivalent values occurred in alternate intra-seasonal periods: January–March, D = 2.40; April–June, D = 3.77; July–September, D = 2.68; October–December, D = 3.75. Both seasons exhibited a similar pattern of variation in fruit diversity (χ^2 = 0.47, P = 0.93, df = 3; Fig. 3A). The minor values mostly resulted from enhanced fruit production by few species from the middle to the end of the wet (*Cecropia pachystachya*, and *Rudgea virburnoides*) or from the middle to the end of the dry season (*Schefflera morototoni*, and *Copaifera*

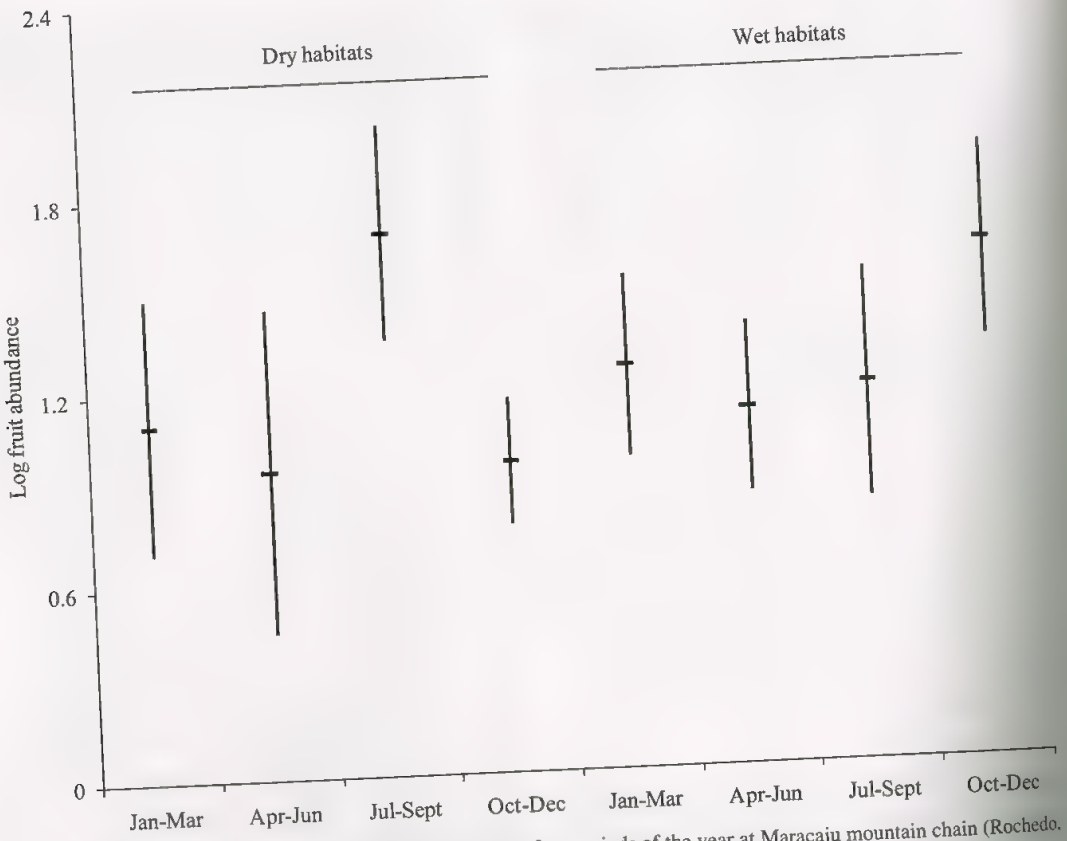

FIG. 1. Fruit abundance in the dry and wet areas in the four periods of the year at Maracaju mountain chain (Rochedo, State of Mato Grosso do Sul, Brazil, 2008; mean ± 1 SD).

langsdoffii, Fig. 3A). Balanced fruit production by more than four species in April–June and October–December amounted for the enhanced diversity values.

Toco Toucan's Use of Food Resources.—I documented 271 feeding records, in which 387 individuals fed on fruits and animal matter in the four habitat types (Table 1, Fig. 4). Toco Toucans foraged on seven fruit species both in the cerrado and streams, six along the river, and five in the deciduous forests. Eight species were common to at least two habitat types (Table 1). Toucans often foraged in the cerrado (87 feeding records, 132 individuals), and streams (93, 118), followed by deciduous forest (48, 69), and river (43, 61). In the course of the year, the proportion of feeding records was different at each habitat type (χ^2 = 101.55, P = 0.001, df = 9, Fig. 4). I observed 21 feeding records in the cerrado during the wet season, while 66 occurred in the dry season. Toucans used both the deciduous forest and river during the dry season (Fig. 4). Toucans foraged more often along the streams during the wet season (Fig. 4). The dry habitats served as major feeding areas in the course of the dry season (105 feeding records), while the wet ones were more important in the rains (Fig. 4). Toucans foraged extensively on abundant fruits (*Schefflera morototoni* and *Copaifera langsdorffii*), during the dry season (38.5% of feeding records, Table 1). In the wet season, they moderately (12.2% of feeding records) fed on a collection of fruit types (Table 1), while extensively foraging on *Nectandra cissiflora* fruits (13.5% feeding records, Table 1). Toucans fed on *Cecropia pachystachya* catkins all year (21.9%, Table 1). Much of the variation associated with the temporal use of different habitat types was a consequence of the consumption of important fruits, which were simultaneously available in more than one habitat type (Table 1). Two coherent groups of fruit species emerged (Correspondence Analysis, Axis 1 = 84.46%, and Axis 2

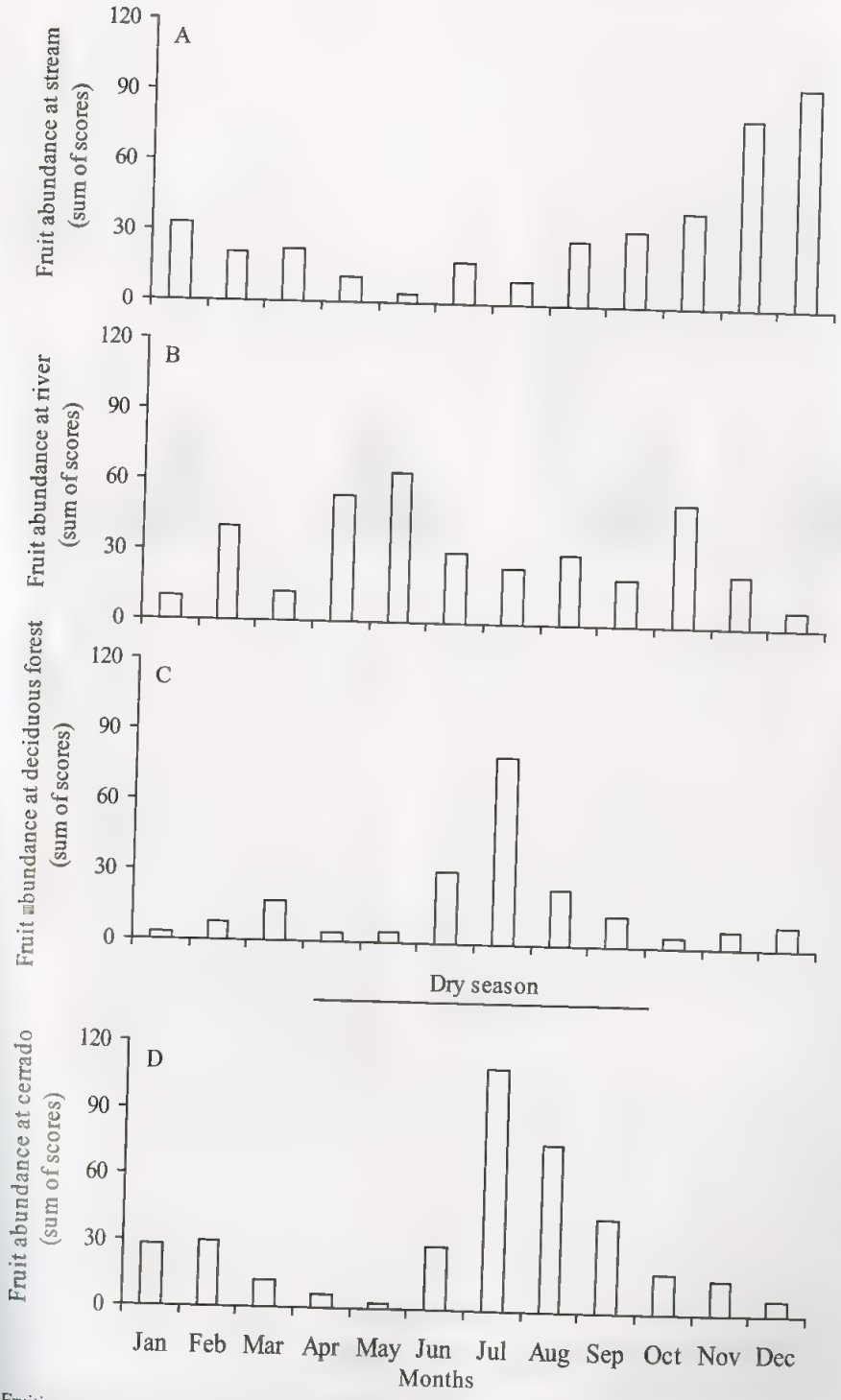

FIG. 2. Fruiting patterns in the four habitat types (A, B, C, and D; see methods), at Maracaju mountain chain (Rochedo, State of Mato Grosso do Sul, Brazil, 2008).

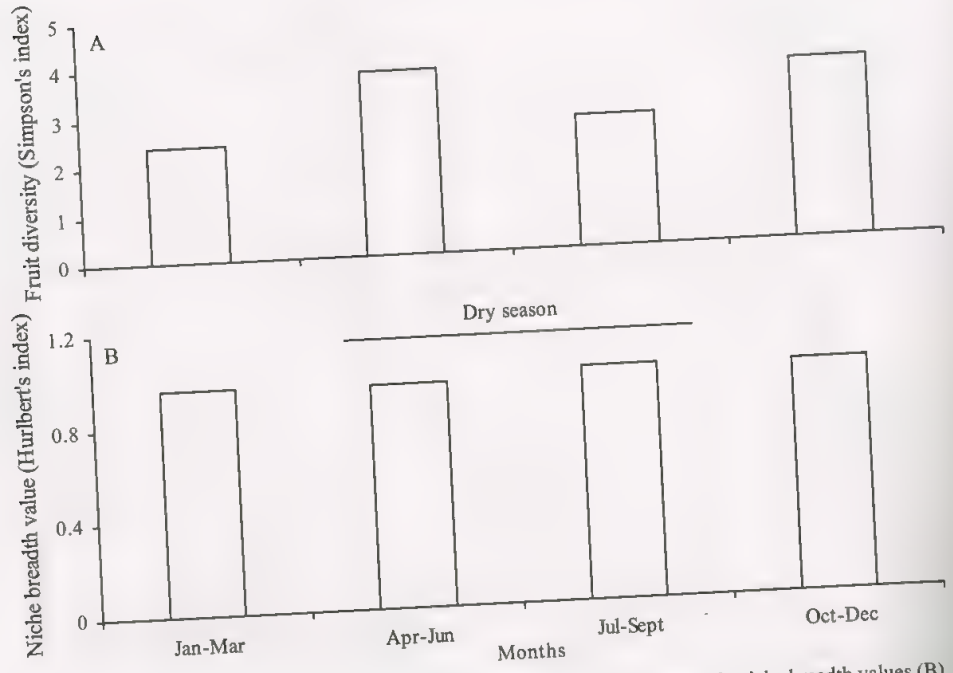

FIG. 3. Variations of Simpson's diversity index (A), of available fruits and Hurlbert's niche breadth values (B), of Toco Toucans' diet during four periods of the year in the Maracaju mountain chain (Rochedo, State of Mato Grosso do Sul, Brazil, 2008).

= 10.42% of the variance associated with feeding area and respective fruit species, Fig. 5). One of them was comprised of *Schefflera morototoni* and *Copaifera langsdorffii*, which toucans exploited mostly in the dry areas. The other included *Nectandra cissiflora*, *Cecropia pachystachya*, and *Guarea guidonea*, exploited mainly along the water courses. Toucans fed on similar proportions of *Xylopia aromatica* either in the borders of streams or cerrado (Fig. 5).

Hurlbert's niche breadth for Toco Toucans exhibited year-round wide values (minimum $B' = 0.95$, Apr–Jun, maximum $B' = 0.99$, Jul–Sept; Fig. 3B). This trend reflected the extensive consumption of a diverse array of abundant fruit species from different habitat types in the four periods of the year (Table 1, Figs. 4, 5).

Toco Toucans fed on arthropods mostly during the rainy season. In the early rains, they captured large green caterpillars (±5–10 cm), on the leaves of cerrado trees. In this period, they also ate the eggs from two bird nests. One of them was a cavity nest in a dead palm used by Turquoise-fronted Parrots (*Amazona aestiva*), while the other, an open nest of Tropical Kingbirds (*Tyrannus melancholicus*).

DISCUSSION

Spatio-temporal Variation in Fruit Availability.—Fruiting was a highly seasonal event across the habitat mosaic. In the dry areas, fruits extensively exploited by Toco Toucans peaked in abundance during the dry season, although the cerrado also produced important fruits in the wet season. The dry areas exhibited large numbers of *Schefflera morototoni*, and mainly *Copaifera langsdoffii* trees (JRN, pers. obs.), which provided fruits for toucans during much of the dry season when fleshy fruits tend to decline in tropical areas (van Shaick et al. 1993). Riparian areas exhibited enhanced fruit production in the course of the wet season as occurs elsewhere in the gallery forests within the cerrado areas (Funch et al. 2002, Ragusa-Netto 2008a). Along the water courses, the most common tree species (*Nectandra cissiflora*, *Cecropia pachystachya* and *Xylopia aromatica*), dominated the fruiting pattern. At a landscape scale, this fruiting asynchrony resulted in year-round fruit availability across the habitat mosaic. These results should be interpreted with care, as I sampled fruit abundance at a relatively small number of sites and do not have replicates

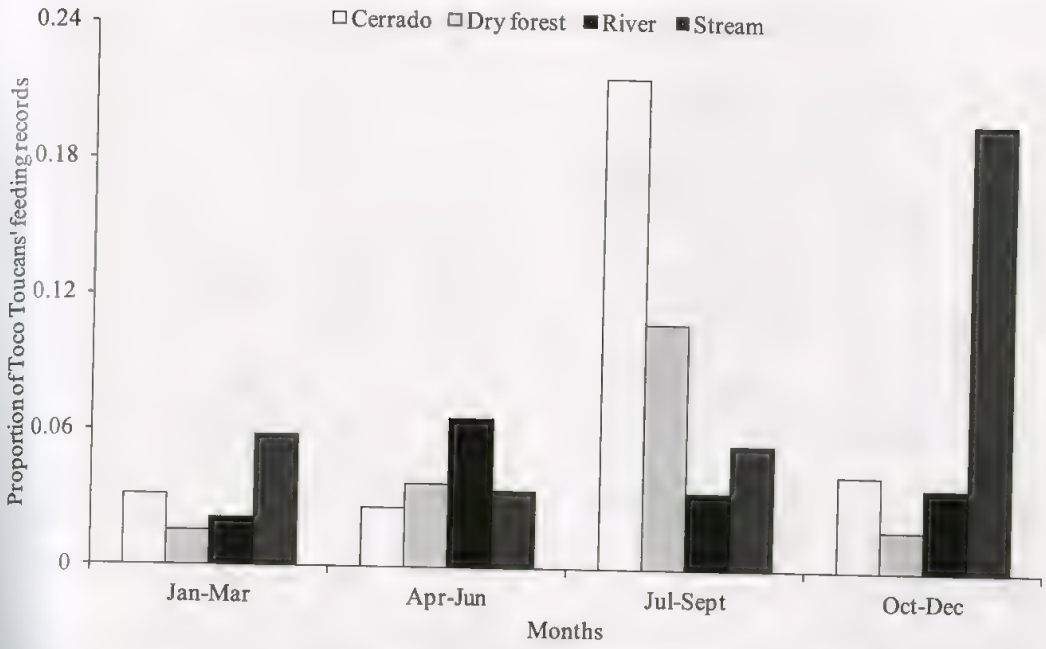

FIG. 4. Proportion of Toco Toucans' (*Ramphastos toco*) feeding records throughout the habitat mosaic in the Maracaju mountain chain during four periods of the year (Rochedo, State of Mato Grosso do Sul, Brazil, 2008).

across years. However, the detection of a substantial number of feeding toucans through the habitat mosaic suggests the need for a rich collection of feeding sites to provide diverse fruit types adequate for the maintenance of toucan populations (van Schaik et al. 1993, Haugaasen and Peres 2007).

Food Plants.—In this present study, toucans fed on six fruit species previously unrecorded either in the cerrado, or seasonal forests (Ragusa-Netto 2006, 2008a, 2010). One of them, *Copaifera langsdorffii*, anecdotally cited in the Toco Toucan's diet (Sick 1997), emerged among their major fruit resources. This tree species is common both in dense cerrado and deciduous forests (Lorenzi 1994); together with *Schefflera morototoni* and *Nectandra cissiflora*, also present in different habitat types, it comprised 52% of feeding records. These fruits were highly abundant and widely distributed, which made them uncommonly important for Toco Toucans, as expected for a feeding generalist (Renton 2001, Walker 2007, Ragusa-Netto 2008a). Five other species (*Curatella americana, Davilla elliptica, Guarea guidonea, Rudgea virbunoides*, and *Xylopia aromatica*), despite being common on the landscape (Lorenzi 1994, 1998), comprised only 12.5% of feeding records. These contrasting proportions demonstrate a common pattern in the diet of toucans, they tend to extensively exploit a few fruit types, while moderately using a larger set of other varieties (Galetti 2000; Ragusa-Netto 2006, 2008a, 2010); this is a pattern also found in the diet of hornbills (Datta and Rawat 2003). The consumption of a diverse array of fruit species might be essential to meet the nutritional requirements of Toco Toucans, since there is high variation in the nutrient content of fleshy fruits (Martínez del Rio and Restrèpo 1993, Corlett 1996).

Major fruits were available for variable lengths of time during the year. Toco Toucans foraged on *Cecropia pachystachya* catkins every month. In the late wet, and early dry season those catkins comprised the bulk of their diet. In the early morning, I often observed groups of toucans arriving and foraging on this tree species. Presumably, the catkins quickly provided much of the energy required to compensate for the overnight fasting. The importance of *C. pachystachya* is suggested by its regular presence in the diet of the toucans, even when fruits of *Schefflera morototoni* and *Copaifera langsdoffii* were plentiful. The toucans combined those fruits to take from them the best caloric and nutritional reward possible (Martínez del Rio and Restrepo 1993).

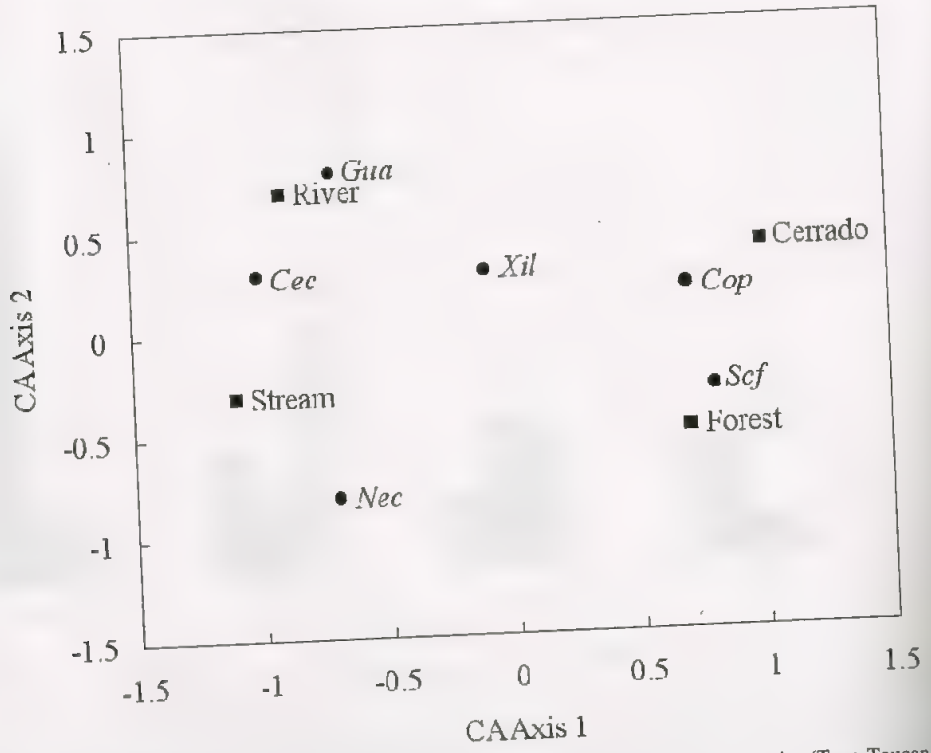

FIG. 5. Correspondence analysis (CA) ordination plot in which the circles denote fruit species (Toco Toucan feeding records) overlapping the habitat types (squares). Fruit species are represented by the first three letters of their genera names (Rochedo, State of Mato Grosso do Sul, Brazil, 2008; see Table 1).

Feeding Between Habitats.—The study site includes a diverse collection of dry and wet cerrado habitats, and toucans move among feeding areas either in response to fruiting peaks, or to exploit particular fruits of a given habitat type. Without radio tracking individual birds, it is difficult to evaluate the extent of inter-habitat movements by toucans (Powell and Bjork 1995, Graham 2001, Holbrook 2011); however, in several instances I observed Toco Toucans flying from one habitat type to another (mainly from the dry to wet ones, and vice versa), when fruits were simultaneously available at those sites. As toucans are well known to exploit large and diverse areas (Graham 2001; Ragusa-Netto 2006, 2008a, 2010; Holbrook 2011), the potential for simultaneous use of different feeding sites in response to fruit availability is plausible. The variations of local occurrence of feeding toucans could be, at least partly, explained by such seasonal inter-habitat movements. Many of them were feeding in the dry habitats during the late dry season, and subsequently at streams in the early wet season, when fruits were plentiful. Moderate numbers of toucans foraged in all habitat types in the absence of pronounced fruiting peak at a given site. This seasonal movement between different types with staggered fruiting peaks, may allow for the persistence, at landscape scale, of Toco Toucans (Ragusa-Netto 2008a, 2010). Fruit diversity was similar between seasons suggesting there is not an abrupt change in the abundance and variability of food supply. Toucans often exploited either dry or wet habitats according to the temporal availability of important food resources (Ragusa-Netto 2008a, 2010). More research is necessary to evaluate the extent to which dry and wet habitats might complement each other in providing fruits for Toco Toucans across their range.

Toco Toucans exhibited wide niche breadth values all year round; this parameter fluctuated moderately because of the consumption of various proportions of diverse fruit types in different periods of the year. In marked seasonal areas, frugivores often exhibit fluctuations of niche breadth values according to the seasonality of

food resources (Renton 2001, Ragusa-Netto 2008a). It is important to emphasize the patchiness in abundance of important fruits. Although I sampled three sites per habitat type, some fruit species were common at only one site. The most pronounced cases were the enhanced *Nectandra cissiflora* fruiting at one stream, *Schefflera morototoni* at one deciduous forest, as well as *Myrcia bella* at one cerrado site. This spatial heterogeneity, potentially, reflected vegetation differences among the four habitat types as well as floristic variations between related sites (van Schaik et al. 1993, Haugaasen and Peres 2007). This suggests the importance of considering the peculiarities of a given area, within a habitat mosaic, which might be a key role in providing fruits in the course of seasons and should be considered in conservation planning for declining species.

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Short Communications

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Rarely Parasitized and Unparasitized Species Mob and Alarm Call to Cuckoos: Implications For Sparrowhawk Mimicry By Brood Parasitic Cuckoos

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ABSTRACT.—Recent experiments support the long-standing hypothesis that Common Cuckoos (*Cuculus canorus*) are mimics of Eurasian Sparrowhawks (*Accipiter nisus*). Additional experiments further suggest that mimicry benefits the cuckoos by reducing the intensity of mobbing they suffer near host nests, at least in some host populations, potentially increasing their access to the hosts' nests. We observed two species of birds—one very rarely parasitized and the other never parasitized by cuckoos—responding to a cuckoo as they would a bird of prey. On the island of Öland, Sweden, we observed two instances of a gray phase cuckoo being mobbed by a group of Barn Swallows (*Hirundo rustica*) during the non-breeding season. These mobbing observations cannot be explained as a consequence of selection in the context of brood parasitism, because swallows are extremely rare cuckoo hosts and should not show co-evolutionary responses to parasitism. Instead, the swallows appear to have mistaken the cuckoos for Eurasian Sparrowhawks and responded as they would to true hawks. Similar observations were made in California, where a vagrant Common Cuckoo repeatedly elicited alarm calls from Bushtits (*Psaltriparus minimus*), a species completely allopatric with cuckoos and thus with no evolutionary history of brood parasitism. Because Eurasian Sparrowhawks visually resemble related North American bird-eating *Accipiter* hawks in plumage and flight characteristics, the cuckoo likely triggered a general *Accipiter* response in the Bushtits. Together, these observations provide additional evidence that cuckoos successfully mimic Eurasian Sparrowhawks and that such mimicry comes not only with benefits to the cuckoos, but costs as well. *Received 2 October 2012. Accepted 2 March 2013.*

Key words: Barn Swallow, brood parasitism, Bushtit, Common Cuckoo, Eurasian Sparrowhawk, hawk mimicry, mobbing.

The costs avian brood parasites impose on their hosts has led to co-evolutionary arms races in a variety of taxa (Rothstein 1990, Davies 2000). Hosts evolve defenses to reduce the risks or costs of parasitism, which in turn favor selection for counter adaptations in the parasites to thwart the host defenses, and vice versa. Many studies of this antagonistic co-evolution have focused on adaptations related to egg recognition and rejection, but there is also growing evidence that host-parasite behavioral interactions before or during the act of parasitism are important as well (Neudorf and Sealy 1992, Feeney et al. 2012). For example, hosts of the Common Cuckoo (*Cuculus canorus*) aggressively defend their nests by mobbing cuckoos (Moksnes et al. 1991, Røskaft et al. 2002, Grim 2005, Honza et al. 2006), and at sites where parasitism is common, hosts that mobbed more intensively were also less likely to be parasitized (Welbergen and Davies 2009).

Intense mobbing is potentially costly to the brood parasites (Welbergen and Davies 2008), and cuckoos appear to have reduced some of these costs by the evolution of plumage traits that mimic a bird predator, the Eurasian Sparrowhawk (*Accipiter nisus*). The strongest evidence for mimicry comes from experimental presentations of cuckoo and sparrowhawk models to two species of titmice not parasitized by cuckoos, and therefore not under selection to recognize cuckoos in the context of parasitism. In both titmouse species, individuals showed similar heightened responses to a hawk and a cuckoo relative to a control mount, implying that the cuckoo successfully mimics the hawk (Davies and Welbergen 2008). Experimental presentations of similar mounts at nests of Eurasian Reed Warblers (*Acrocephalus scirpaceus*), a species parasitized by cuckoos, showed that the hosts are particularly aggressive to cuckoos. However, experimental alteration of the presence or absence of the barred breast pattern on the cuckoo—a plumage trait shared with the hawks—affected the intensity of aggression shown by hosts (Welbergen and Davies 2011). Taken together, these studies provide convincing evidence that specific aspects of cuckoo plumage mimic features of sparrow-

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hawks, and that the mimicry benefits the cuckoos. Here, we describe observations that provide additional evidence that cuckoos are sometimes mistaken for sparrowhawks or other similar *Accipiter* hawks by two bird species that should not be under selection from brood parasitism, a very rarely parasitized species and an unparasitized species. These observations also suggest that by mimicking hawks, cuckoos may incur costs not directly connected to brood parasitism.

OBSERVATIONS

We observed two instances of a flock of Barn Swallows (*Hirundo rustica*) mobbing a lone cuckoo in Sweden during the non-breeding season (BEL, pers. obs.) and one instance of a cuckoo repeatedly eliciting alarm calls from a flock of Bushtits (*Psaltriparus minimus*; GSG, pers. obs.) in California, USA. We observed the swallows 2.4 km north of the Ottenby Bird Observatory at the southern tip of the island of Öland, southeastern Sweden, an area known to be a migratory hotspot for many birds. This area is mostly open heath with scattered short trees and bushes, but there is also a large patch of woodland adjacent to where we made the observations. The observation of the Bushtits was made in Watsonville, California, in riparian habitat with a mixture of dense patches of willows (*Salix* sp.) and open areas.

On 10 August 2012, at approximately 0800, we were observing migrant birds at the edge of a small patch of woodland surrounded by heath. A group of 30–40 Barn Swallows was intermittently switching between perching on a tree and foraging in the air nearby (we therefore, had a sense of the maximum number of swallows in the area). Our attention was caught by a sudden burst of alarm calls and we looked up to see some of the swallows aggressively mobbing a larger bird that was flying towards us. The swallows were calling excitedly and several individuals dive-bombed the larger bird. The vocalizations and dive-bombing behavior were similar to the mobbing behavior we observed several times in North American populations of Barn Swallows in the presence of a raptor. The mobbed bird eventually flew close enough (30 m) that we could see clearly that it was a gray phase Common Cuckoo. The swallows continued to mob the cuckoo aggressively until it looped around and returned to the trees, in what appeared to be an evasive maneuver. The entire interaction lasted approximately 10 secs. Thirty minutes later we observed another mobbing event at the same place, but this time the swallows mobbed a real Eurasian Sparrowhawk. Their behavior towards the real hawk seemed identical to their treatment of the cuckoo.

The next day (11 Aug 2012, at ~0830) we observed another mobbing incident between swallows and a cuckoo, at the same location. As before, our attention was initially drawn to mobbing vocalizations and we noticed a group of approximately 15–30 Barn Swallows mobbing a gray bird in flight. We were initially convinced that the bird was a sparrowhawk, but when it flew sufficiently close (again ~30 m) we could see that it was a gray phase cuckoo. The bird appeared to take evasive action to avoid the swallows by suddenly changing direction and flying rapidly about 150 m across an open area before disappearing into a large tree (distance estimated from the locations of individual trees on Google Earth). It remained hidden in the tree for 5 mins but flushed when we approached the tree, and it then flew across an open area towards a large patch of forest.

On 29 September 2012 in the early afternoon, a hepatic plumage cuckoo was observed in wetlands near Watsonville, California. Common Cuckoos are very rare vagrants to North America, so there were a couple of dozen birdwatchers at the site observing the bird's every movement. The cuckoo was generally hidden from view in the willows. However, it came into view three times over a period of 15 mins when it briefly flew out into the open before disappearing into the willows again. Each time the cuckoo flew into the open, a flock with at least 10 Bushtits erupted in their loud and distinctive alarm calls. Bushtits frequently give these calls in the presence of avian predators (Sloane 2001), and we have frequently observed flocks of Bushtits in central California giving these alarm calls when Cooper's Hawks (*Accipter cooperii*) fly by. Some of the birdwatchers in the group also commented that they found the Bushtits' response to the cuckoo similar to the manner in which Bushtits may respond to Cooper's Hawks.

DISCUSSION

These observations add to the very limited published evidence that birds respond aggressively to cuckoos as hawk mimics, and not just as brood parasites. They also highlight the need to consider that hawk mimicry may come with fitness costs as well as benefits. Naturalists have

long noted a resemblance between Common Cuckoos and Eurasian Sparrowhawks, both in terms of plumage features and flight characteristics. Ash (1965), for example, described several instances where the flight characteristics of Common Cuckoos were very similar to those of sparrowhawks, including the characteristic flap-gliding flight pattern typical of *Accipiter* hawks in general. Ash also noted that the hawk-like flights often seemed to be associated with visits to potential host nests, and in some cases they were specifically associated with parasitic egg-laying. However, he concluded that the resemblance to raptor flight was 'fortuitous'—because of the aerodynamic aspects of flight—rather than because of mimicry. The recent studies of hawk mimicry by cuckoos, however, suggest that this resemblance to raptor flight might make sense in terms of cuckoo mimicry of the raptors.

In a series of elegant experiments Welbergen and Davies (Welbergen and Davies 2008, 2009, 2011, 2012; Davies and Welbergen 2008, 2009) provide clear evidence that cuckoos mimic Eurasian Sparrowhawks, at least in some plumage features, and that such mimicry affects the way that cuckoos are treated by some hosts. Enemy recognition, in general, is typically assessed by how victims respond to a putative enemy. Davies and Welbergen (2008) assessed the responses of Great Tits (*Parus major*) and Eurasian Blue Tits (*Cyanistes caeruleus*)—both species are unsuitable as hosts and not parasitized by cuckoos—to cuckoo and hawk mounts placed at feeders during the winter, when cuckoos were absent. Individuals in both species showed similar responses to cuckoo and sparrowhawk mounts—high rates of alarm calls and avoidance of the feeder—but very little response to a dove mount (the control). Moreover, experimentally altering aspects of the cuckoo plumage revealed that the barred breast pattern in particular caused a similar response to both the cuckoo and hawk models, and hence is a critical component of the mimicry. The observation that these two titmice respond similarly to cuckoo and hawk mounts, coupled with the fact that they are unsuitable cuckoo hosts (they nest in small holes inaccessible to cuckoos) so their responses to cuckoos cannot be explained by selection from brood parasitism, provides powerful evidence for hawk mimicry by cuckoos.

Our observations of two other species showing classic anti-predator responses to cuckoos—mobbing a cuckoo in flight (swallows) or alarm calling when a cuckoo flew (Bushtits)—provides additional, independent support for the hypothesis that cuckoos mimic hawks. Swallows have traditionally been considered as unsuitable hosts for cuckoos, but there are a few dozen records of cuckoo chicks in swallow nests (T. Grim, pers. comm.). Nonetheless, the scarcity of such records compared to those for more typical hosts suggests that parasitism of swallows is so rare that their response is very unlikely to be a selected anti-parasite response. Moreover, our observations were made during the non-breeding season. Bushtits provide a more striking example, because they are fully allopatric with Common Cuckoos, including breeding and wintering. We do not know what cues triggered the responses in the swallows and Bushtits. Although the observations in both species involved cuckoos in flight, in neither case were the cuckoos adopting an *Accipiter*-like flap and glide flight profile. However, *Accipiter* hawks themselves do not always adopt flap and glide flight, so it is not a prerequisite for effective mimicry.

Given that many birds mob hawks, it is somewhat counterintuitive that cuckoos that mimic hawks can benefit in the context of brood parasitism. Cuckoo hosts will aggressively mob cuckoos—particularly when they have learned through social transmission to distinguish cuckoos from hawks. However, inexperienced hosts seem to be more wary of hawks, and it is in this context that mimicry of sparrowhawks appears to reduce the intensity of mobbing by hosts (Welbergen and Davies 2009). Welbergen and Davies (2009) also suggest that this reduction in mobbing may make it easier for the cuckoos to successfully access host nests.

Our observations suggest that the traits that benefit cuckoos by reducing their mobbing intensity at host nests may also bring costs in terms of higher mobbing rates or intensities outside the context of brood parasitism. Moreover, these costs are to be expected anywhere (including wintering areas) that cuckoos are sympatric with Eurasian Sparrowhawks or other similar *Accipiter* hawk species. The fitness costs of being mobbed are not known for birds in general, but studies of mobbing in hawks and owls show that mobbing can have dramatic effects on the behavior of the mobbed individuals, including where they choose to roost to reduce the risk of being mobbed (Hendrichsen et al. 2006) and moving away from foraging areas after being mobbed (Pettifor 1990).

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Using Morphometric Measurements to Estimate Age of Nestling Red-shouldered Hawks in Two Eastern Populations

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ABSTRACT.—Nestling growth may be used to estimate age of nestling raptors, which is valuable for investigating hatch order dynamics and nestling behavior, as well as assessing reproductive rate and back-calculating hatching date. To estimate nestling age, the most valuable parameter to measure growth is one that does not vary greatly with environmental factors, and ideally is applicable over a wide range of populations. We measured growth of nestling Red-shouldered Hawks (*Buteo lineatus*) in Quebec, Canada, from ages 3 days to near fledging (38 days old), and compared growth of several parameters in different size broods. As a validation study, we measured similar parameters one time in known-age nestling Red-shouldered

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Hawks in southwestern Ohio. Growth rates for tarsus length, bill length, and tail length differed between nestlings in broods of one and three young, respectively, in Quebec. However, mass gain and growth of secondary feathers (mean length of first and second secondaries) did not differ between brood sizes, although mass gain was more variable than secondary growth. These results suggested that secondary feather length was the most valuable parameter for estimating nestling age in Red-shouldered Hawks. Comparing Ohio nestlings to Quebec nestlings, we found that growth of secondary feathers differed significantly, with Ohio nestlings having smaller secondary length, relative to age estimate. Application of the equation generated with the Quebec data to estimate the age of the Ohio nestlings based on secondary length resulted in estimates that were 2.3 ± 0.3 days (range 0.25–4.5 days; n = 22) younger than the Ohio nestlings' actual ages. Based on this validation study, we suggest that the use of the Quebec age-secondary length equation to estimate age for nestling Red-shouldered Hawks in other parts of eastern North America is acceptable, though with the caveat that such estimates are associated with potential small errors. *Received 24 January 2013. Accepted 3 May 2013.*

Key words: ageing, breeding, brood size, *Buteo lineatus*, growth, morphometrics, nestling, Red-shouldered Hawk.

Relatively little quantitative information exists on the growth of nestling raptors in the wild (Penteriani et al. 2005), in part because of the disturbance required for repeated measurements of nestlings (Penteriani et al. 2005, Rosenfield et al. 2007). Nestling growth rates may be an indicator of important ecological factors such as habitat quality (Bortolotti 1989, Hanauska-Brown et al. 2003) and feeding rates (Ricklefs 1983, Bortolotti 1989). Knowledge of typical growth rates may be important baseline information for future studies, in which environmental stressors including contaminants and reduced food availability could potentially affect nestling growth. Nestling growth may also be used to estimate age of nestlings (Bortolotti 1984, Poole 1989, Penteriani et al. 2005, Pande et al. 2011), which is valuable for understanding hatch order dynamics and nestling behavior, for back-calculating hatching date, for assessing reproductive rate, and for use as a covariate in ecological or toxicological studies of nestlings.

If nestling growth is to be used to estimate nestling age, it is important to understand which environmental factors can affect growth. It is plausible that feeding rates would affect growth of some or all measured parameters (Ricklefs 1983, Lacombe et al. 1994, McDonald 2003). In addition, brood size may influence growth rates (e.g., Stinson 1977, Dijkstra et al. 1990, Gard and Bird 1992), and brood/clutch size may be dependent on other factors such as the amount of food available, the quality of the breeding pair, or the quality of the territory (Masman et al. 1989). For estimating nestling age, the most valuable parameter to measure growth would be one that does not vary greatly with environmental factors (Eriksson et al. 1984), and ideally is applicable over a wide range of populations.

The growth of feathers, particularly primary feathers, has been used to reliably estimate nestling ages in other raptor species in the wild, including Bald Eagles (*Haliaeetus leucocephalus*: eighth primary; Bortolotti 1984), Red-tailed Hawks (*Buteo jamaicensis*: fourth primary; Bechard et al. 1985), Bonelli's Eagles (*Aquila fasciata*: seventh primary; Mañosa et al. 1995), Gyrfalcons (*Falco rusticolus*: seventh primary; Poole 1989), and Turkey (*Cathartes aura*) and Black vultures (*Coragyps atratus*: fourth primary; Coleman and Fraser 1989). Wing length (flattened wing chord) was used to estimate age in Brown Falcons (*F. berigora*; McDonald 2003). In addition, in other studies, primary growth rate was nearly constant (Donazar and Ceballos 1989), and primary growth tended to be unrelated to environmental and dietary stresses (Petersen and Thompson 1977, Olsen and Olsen 1987). The strong age-feather length relationships observed in a variety of species, and the limited influence of environmental variables indicate that flight feather growth takes priority over other, more-flexible growth parameters, such as mass (Coleman and Fraser 1989, Donazar and Ceballos 1989, Negro et al. 1994, McDonald 2003). However, no studies have examined growth of morphologic features in nestling Red-shouldered Hawks (*B. lineatus*).

The influence of brood size on growth rate has been examined in several species of raptors. Growth rate was independent of brood size in Eurasian Sparrowhawks (*Accipiter nisus*; Newton 1978, Moss 1979), American Kestrels (*F. sparverius*; Balgooyen 1976), and Ospreys (*Pandion haliaetus*) in Nova Scotia, Canada (Schaadt and Bird 1993). However, an inverse relationship existed between brood size and fledging mass of Ospreys in Virginia, USA, in a study in which some broods were experimentally enlarged (Stinson 1977). Understanding the effects of brood size on growth rates of various morphological param-

eters is important for selecting appropriate parameters to estimate nestling age.

Our objectives in this study were (1) to evaluate the effects of brood size on growth, and (2) to determine which morphological measurements may be used to estimate age in nestling Red-shouldered Hawks.

METHODS

Study Areas.—Our primary study area consisted of a forested region of approximately 200 km^2 in the northwestern corner of Vaudreuil County (45° 15′ N, 74° 26′ W), southwestern Quebec, about 45 km southwest of Montreal. Dominant vegetation included mature stands of sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*), as well as yellow birch (*Betula alleghaniensis*), white ash (*Fraxinus americana*), American basswood (*Tilia americana*), bigtooth aspen (*Populus grandidentata*), red maple (*A. rubrum*), and oaks (*Quercus* spp.). The region has been previously described in detail (Morris and Lemon 1983).

One additional nest was located in the demonstration forest (2.0 km^2) of the Morgan Arboretum (45° 57′ N, 74° 26′ W), Macdonald Campus of McGill University, located approximately 30 km east of the main study area. Dominant tree associations were similar to those described for the main study area.

A secondary study area was located in southwestern Ohio, in the suburbs surrounding the city of Cincinnati (approx. 39° 9.7′ N, 84° 27.4′ W). A description of the study area has been published (Dykstra et al. 2000, 2004). Data collected in this study area were considered a *post-hoc* validation trial for the morphological data analyzed at the primary study area.

Quebec Study.—Before leaf-out in the spring of 1979 and 1980, BLP searched Red-shouldered Hawk territories that had been occupied in previous years, as well as areas where Red-shouldered Hawks were observed or heard. Nests with incubating adults were considered active.

In 1980, eight nests in the primary study area and one nest in the Morgan Arboretum were selected for this study. Nests were visited every 4–7 days during May and June to weigh and measure the young. To create a larger range of brood sizes, two nests were manipulated: one nestling was removed from a brood of three and transferred to another nest originally containing three young. Initial brood size of all nests was 3–4 young, but mortalities occurred in all nests except one. We analyzed growth data only of nestlings that survived to fledging. The brood size used in the analyses was that which existed for at least half (17 days) of the nestling period. Nestlings were lowered to the ground where body parameters were measured. No nestlings were measured on rainy or cold overcast days to avoid potential hypothermia.

Approximate hatching dates were determined by observations made either directly by climbing the nest tree or an adjacent tree, or indirectly from the ground using a spotting scope. Estimates of nestling age were accurate to about ±2 days. Masses at hatching were determined from two nestlings, each from a different nest. Nestlings were weighed with Pesola spring scales. Crop fullness was estimated visually as 0.25, 0.50, 0.75, or completely full (Schaadt and Bird 1993). The mass of a full crop was measured in a dead nestling, and the total body mass of each individual nestling was adjusted to account for crop fullness where applicable. It was assumed that the crop represented a constant percentage of body mass throughout development (G. Duke, pers. comm.).

We measured the following parameters to the nearest 0.1 mm with vernier calipers or nearest mm with a 30-cm wooden ruler: bill length, tarsus length, the length of the first two secondary feathers, and the length of the central two retrices. Bill length was measured including the cere. Tarsus was measured as in Olendorff (1972) and Schaadt and Bird (1993) from the heel to the joint between the distal end of the tarso-metatarsus and the middle toe, which included the portion of the tibio-fibula that overlapped with the tarso-metatarsus. Feathers were measured from the point of insertion to the tip of the flattened feather (Olendorff 1972, Pyle 2008). Red-shouldered Hawk nestlings were not sexed.

Southwestern Ohio Validation Study.—Nest sites were known to us from prior studies (Dykstra et al. 2000, 2004, 2009). At three nests in 2011 and six nests in 2012, 24-hr time-lapse infrared video cameras (mono-power color/infra-red video camera [PC177IRHR-8] and mini-DVR [MDVR14-4] from Supercircuits, Austin, Texas, USA) were mounted above occupied nests of Red-shouldered Hawks prior to egg-laying. Exact hatch date for each nestling in these nests was determined by review of the recorded images. Brood sizes were initially 1–3 young, and we banded and measured all nestlings (as above) that survived to age 21–28 days. Each nestling was measured one time. For more study details, see Miller (2013).

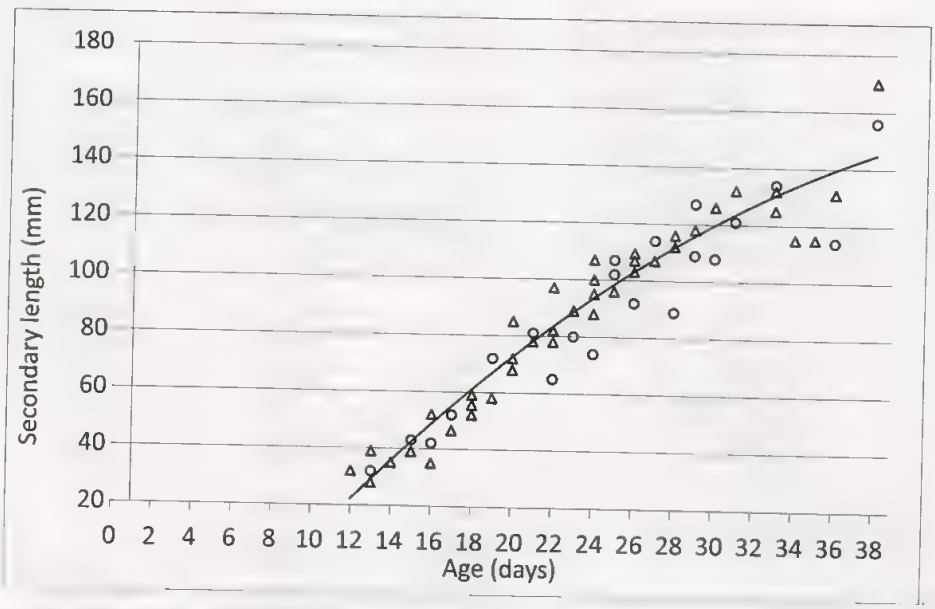

FIG 1. Mean length of first and second secondary as a function of age for nestling Red-shouldered Hawks in Quebec, Canada. Triangles = brood size of 1; circles = brood size of 3. Equation: $y = -67.8 + 8.49x - 0.077x^2$; $R^2 = 0.92$; $P < 0.001$, $F_{2,58} = 315.4$; y = secondary length in mm, x = age in d.

Statistical Analyses.—To describe growth patterns relative to nestling age for nestlings in Quebec, we used stepwise GLM analysis with some exponential terms, as well as an interaction between brood size and age. To compare nestlings in Ohio to nestlings in Quebec, we included all nestlings and used stepwise GLM analysis to test the relationship of secondary length with nestling age, with the addition of a variable for location (Quebec vs. Ohio). *P*-values <0.05 were considered significant. Analyses were performed with SAS (Barr et al. 1976) and Systat software (Systat 2009).

RESULTS

Nestlings in Quebec.—We measured growth of 14 nestlings in nests with final brood size of one young ($n = 5$ nests) or three young ($n = 3$ nests; Penak 1982); a single nest with a final brood size of two young was excluded from further analysis to facilitate comparison of large vs. small broods. Growth curves for most of the body parameters were generally sigmoid in shape. Growth of the wing feathers (first and second secondary) did not differ between brood sizes one and three in Quebec (Fig. 1) and could be described well by a quadratic equation that included a term for age and one for age*age. Mass gain by nestlings in Quebec also did not differ between brood sizes (Fig. 2), although variability was greater.

Growth of the bill, tarsus, and tail feathers differed significantly among broods of three and broods of one (Table 1). For all three parameters, measurements were larger in nestlings from broods of three than in those from broods of one.

Validation Study in Ohio.—We measured 22 nestlings in nine nests. Brood sizes in these nests at the time we measured the nestlings were one young ($n = 1$ nest), two young ($n = 3$ nests, including a nest in which one of the three young was depredated at age 19 days), and three young ($n = 5$ nests).

Growth of secondary feathers differed between nestlings in Ohio and Quebec (significant variables included in the final model: age, age*age, location; $F_{3,79} = 253.5$; $P < 0.001$; $R^2 = 0.91$), with nestlings in Ohio having smaller mean secondary length than nestlings in Quebec (Fig. 3), relative to age estimate. Using the equation generated with the nestling data from Quebec to estimate the age of the nestlings in Ohio based on secondary length, resulted in estimates that were 2.3 ± 0.3 days (range 0.25–4.5 days; $n = 22$) younger than the nestlings' actual ages. We did not use other parameters to test estimates of age for Ohio nestlings, because other parameters varied with

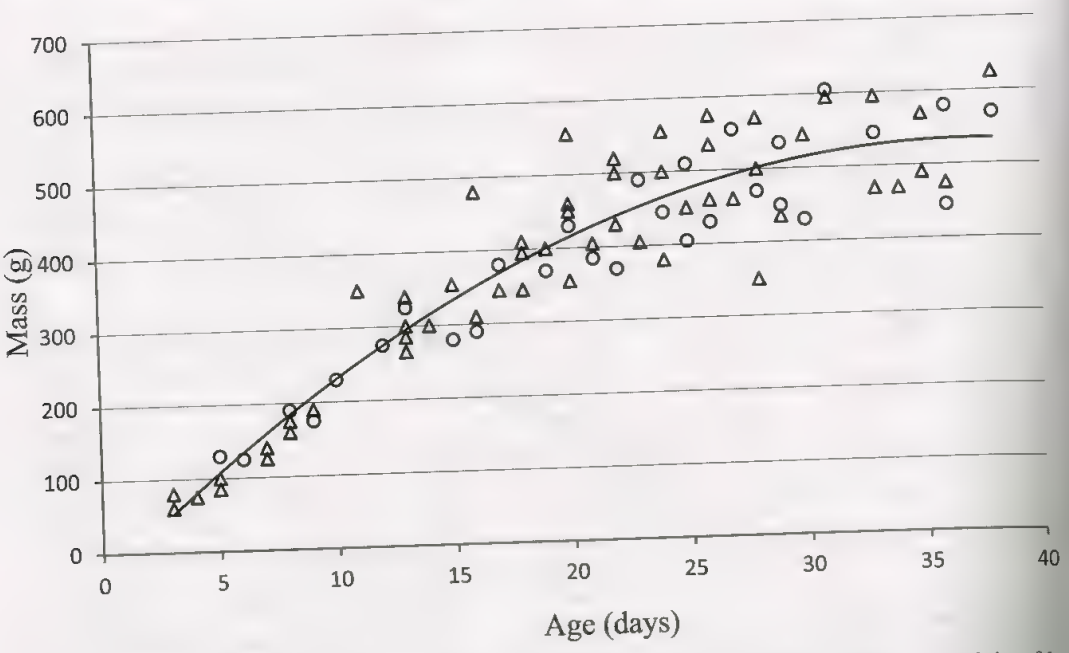

FIG. 2. Nestling mass as a function of age for Red-shouldered Hawks in Quebec, Canada. Triangles = brood size of 1; circles = brood size of 3. Equation: $y = -37.1 + 31.03x - 0.421x^2$; $R^2 = 0.87$; $P < 0.001$, $F_{2,80} = 263.3$; y = mass in g, x = age in d.

brood size (bill length, tarsus, tail length) or were too variable (mass).

DISCUSSION

Comparison of Nestling Growth in Quebec and Ohio.—Based on this validation study, we suggest that the use of the Quebec age-secondary length equation to estimate age for nestling Red-shouldered Hawks in other regions is acceptable, though with the caveat that such estimates are associated with potential small errors. Age-estimates based on secondaries will be more precise than those based on mass, and are not influenced by external factors such as brood size, making them the most appropriate and useful for field studies.

The fact that such estimates consistently underestimated age of nestlings in Ohio (i.e., feathers from nestlings in Ohio were smaller than those of nestlings in Quebec, relative to age) suggests that there may be a systematic difference between the Red-shouldered Hawks in Ohio and Quebec. One possibility is that the hawks in Quebec are larger than those in Ohio, a clinal difference that would agree with the classical Bergmann's rule (Bergmann 1847). Penak (1982) found limited data suggesting that hatchlings in Quebec were larger than those in Maryland (40 g [$n = 2$] vs. 27 g [$n = 1$], respectively; Janik 1980).

A second possibility is that we systematically underestimated the age of nestlings in Quebec. We believe that our estimates were correct to within ± 2 days; however, as hatch dates for some of our nests were determined by watching adult behavior with a spotting scope, we acknowledge that we may not have noticed hatch on the first

TABLE 1. Growth of bill length, tarsus, and tail feathers for nestling Red-shouldered Hawks in Quebec, Canada.

Measurement	Equation[a]	F	R^2	P
Bill length (mm)	$Y = 15.37 + 0.632a - 0.0094a^2 + 0.021ab$	$F_{3,85} = 168.9$	0.85	<0.05
Tarsus (mm)	$Y = 9.82 + 3.93a - 0.061a^2 + 0.027ab$	$F_{3,85} = 901.0$	0.97	<0.05
Tail feather length (mm)	$Y = 80.71 + 8.06a - 0.072a^2 + 2.64b$	$F_{3,53} = 4.32$	0.86	<0.05

[a] y = body parameter; a = age; b = brood size

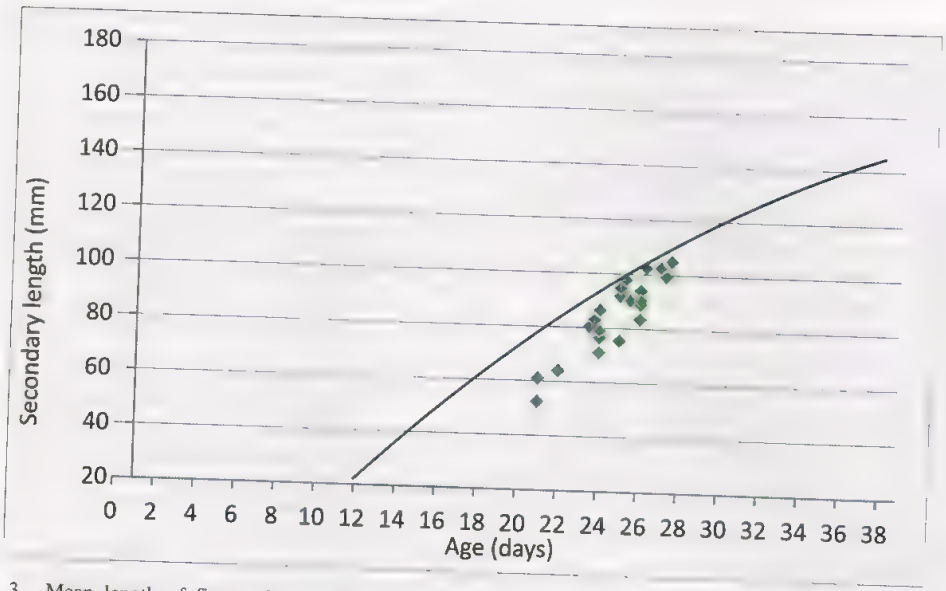

FIG. 3. Mean length of first and second secondary as a function of age for nestling Red-shouldered Hawks in southwestern Ohio, compared to the trendline for nestlings in Quebec (from Fig. 1). Filled diamonds = Ohio nestlings in broods of 1, 2, and 3 (n = 22).

day at every nest. When nestlings are very young, it is possible that brooding may be mistaken for incubation when observers are viewing from the ground. Another important consideration is that hatching is asynchronous in Red-shouldered Hawks, and the hatching dates of the nestlings, particularly the later-hatched nestlings, may be difficult to detect from the ground. In Ohio, hatching intervals were unequal: the second nestling hatched 0.56 days (range 0.04–1.2 days; n = 8) after the first, but the third hatched 1.48 d (range 0.5–2.13; n = 8) after the second (Miller 2013).

In other species, there was some evidence that emergence of the primaries was delayed in the last-hatched (second-hatched) nestling Egyptian Vultures (*Neophron percnopterus*; Donazar and Ceballos 1989), and in female Bald Eagles compared to males (Bortolotti 1984). However, our sample size of third-hatched birds was too small to adequately test for such differences.

Effect of Brood Size on Growth.—In our study, brood size influenced growth rates of some nestling body parameters, but not others, although the differences were small. Other researchers have found similarly inconsistent results. Growth (in mass) of nestling Ospreys was not related to brood size (Schaadt and Bird 1993) in one location, although brood size and fledging mass were negatively correlated in another location, at which some broods were artificially increased to five young (Stinson 1977). Growth rate (mass) for Northern Goshawks (*Accipiter gentilis*) did not vary with brood size, although samples were small (Hanauska-Brown et al. 2003). In American Kestrels for which brood sizes had been experimentally manipulated, growth rates (mass) of females in larger broods were lower than those in control or reduced broods, and ninth primary length in young from enlarged broods was smaller than that in young from smaller broods; however, tarsus length did not differ among brood sizes (Gard and Bird 1992). Similarly, Eurasian Kestrels in experimentally enlarged broods had lower growth rates in terms of mass and wing length (Dijkstra et al. 1990).

In Quebec, brood size also influenced parental behavior of Red-shouldered Hawks. The amount of time spent brooding was greater for broods of three than for broods of one (Penak 1982). In addition, broods of three nestlings were fed more frequently and adults delivered prey of greater mass to broods of three than to broods of one nestling (Penak 1982). Thus, nestlings in broods of three likely experienced thermoregulatory advantages as well as higher energy intake, and these advantages may have permitted them to grow more rapidly, at least in terms of some body parameters. It is not clear why parents of broods

of three would be able to both spend more time brooding and provide more food than parents of one; differences may reflect qualities of the individual birds or territories. In some raptors, more productive pairs were also the most experienced and/or were holding the highest-quality territories (Newton 1979, 1991; Kostrzewa 1996). However, we also note that the study area in Quebec is near the northern edge of the species' range in eastern North America (Dykstra et al. 2008), which implies that habitat quality in general may have been low (Penak 1982). Additionally, there was mortality in eight of nine nests in Quebec (compared to five of nine nests in Ohio; Miller 2013), and the nestlings in broods of one were all the survivors from broods of three. Such significant mortality suggests that either parental quality or territory quality for these nests may have been substandard.

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Recent Sightings of Kirtland's Warblers on San Salvador Island, The Bahamas

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ABSTRACT.—Here we present recent accounts of Kirtland's Warblers (*Setophaga kirtlandii*) captured and observed on San Salvador Island, The Bahamas, in 2012 and 2013. We conducted mist-netting and passive surveys in a variety of habitats on the island from January–March 2012 and December 2012–March 2013. We captured four warblers and sighted at least six other individuals, including two color-banded birds originally banded near Mack Lake, Michigan, USA. Warblers were primarily captured or observed in coastal scrub and inland low coppice habitats where vegetation height is <4 m, has a scrub/shrub appearance, and openings because of disturbance. These habitats are similar to habitats preferred by Kirtland's Warblers on other Bahamian islands, and also have fruiting plants the warblers prefer such as *Erithalis fruticosa*, and *Lantana involucrata*. To our knowledge, these are the first confirmed cases of observed Kirtland's Warblers on the

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island in over 46 years. *Received 11 January 2013. Accepted 7 April 2013.*

Key words: Bahamas, Kirtland's Warbler, San Salvador Island, *Setophaga kirtlandii*, wintering.

The Kirtland's Warbler (*Setophaga kirtlandii*) is a federally endangered Neotropical migrant bird that breeds in Michigan, Wisconsin, and Ontario (Probst et al. 2003, Richard 2008, Trick et al. 2008). Range-wide surveys on the non-breeding grounds indicate that the Bahamian archipelago is the center of Kirtland's Warbler distribution, with the majority of past sightings on Grand Bahama, New Providence, and Abaco, as well as more recent sightings from research conducted on Eleuthera (Haney et al. 1998, Sykes and Clench 1998, Wunderle et al. 2010). Here we present accounts of Kirtland's Warblers observed and captured in their wintering grounds on San Salvador Island, The Bahamas. We also present a description of the habitats in which these individuals were sighted, and compare them to other wintering habitats Kirtland's Warblers have previously been found utilizing. To our knowledge, these are the first confirmed cases of observed Kirtland's Warblers on the island since 1965 (Haney et al. 1998).

All of these sightings were observed incidentally as part of a larger study examining the wintering ecology of Prairie Warblers (*Setophaga discolor*) and other migratory birds on San Salvador Island, The Bahamas. The study encompassed a number of different habitat types, including two sites in coastal scrub habitat totaling about 13 hectares in size. These plots consist of plant species such as *Reynosia septentrionalis*, *Croton linearis*, *Erithalis fruticosa*, *Pithecellobium keyense*, *Bourreria ovata*, *Lantana involucrata*, and many other shrubby woody vegetation species and vines (Smith 1986, Sykes and Clench 1998). All of these species are low growing, resulting in dense vegetation ranging between 1–4 m in height. These sites were located within 600 m east and west of the Gerace Research Centre (24° 07′ N, 74° 27′ W) (Fig. 1).

Two additional sites (''GRC'' and ''RHP'') were located south of the GRC. The 3 ha GRC plot (vegetation height ranging from 2–6 m) consists of plant species such as *Leucaena leucocephala*, *Casuarina equisetifolia*, *Corchorus hirsutus*, *Pluchea odorata*, and *Prunus amygdalus*. The RHP plot, 350 linear meters in size (vegetation height ranging from 2–3 m), consists of short dense broadleaf vegetation (known as coppice), and *Rhizophora mangle*.

A fifth and sixth site (''Jake Jones Road'' and ''Little Lake'') were located in the northwest part of the island. Jake Jones Road (24° 06′ N, 74° 30′ W), a 6-ha plot (vegetation height ranging from 1–8 m), consists of a mosaic of wet and drier areas with plant species such as *Rhizophora mangle*, *Sabal palmetto*, *Conocarpus erectus*, *Chrysobalanus icaco*, tall coppice (4–8 m) dominated by *Eugenia foetida*, *Metopium toxiferum*, and *Hippomane mancinella*, as well as upland areas with inland low coppice (1–4 m) with *Phyllanthus epiphyllanthus*, *Amyris elemifera*, and *Croton eluteria*. Located to the south of Jake Jones Road, the 8-ha site at Little Lake (24° 05′ N, 74° 30′ W) consists of tall coppice, *Conocarpus erectus*, and *Rhizophora mangle* surrounding a lake. Low coppice is present along ridges on the north, south, and west sides of the lake.

Finally, a seventh site known as ''FM'' (24° 03′ N, 74° 31′ W), is located adjacent to lakes and consists of patches of *Conocarpus erectus* and *Cladium jamaicense*. However, within the 7-ha plot there were also patches of low coppice, areas with vegetation such as *Leucaena leucocephala*, *Schinus terebinthifolius*, and *Casuarina equisetifolia*, and areas with coastal scrub vegetation. Vegetation heights within the site were highly variable, ranging on average from 1–10 m, although some scattered *Casuarina equisetifolia* were up to 15 m in height.

Mist-netting and surveys were conducted in every plot except for Jake Jones Road and Little Lake from early January–late March 2012, and in all plots from late December–March 2013. Mist-netting was done mainly in January and March, while surveys were mostly conducted in February. Point counts were also conducted during February of 2012. We quantified netting, point count, and survey efforts for each plot within each year (Table 1). Amongst both years and all study plots, we conducted over 3,000 12-m net-hours, 300 survey hours, and eight point count hours. Net-hours consisted of both target netting (using playback calls of Prairie Warblers and White-eyed Vireos (*Vireo griseus*) to lure birds toward nets) and passive netting.

On 24 January 2012, we captured a Kirtland's Warbler on San Salvador Island in the coastal scrub just west of the GRC. We determined the individual to be an after-second-year (ASY)

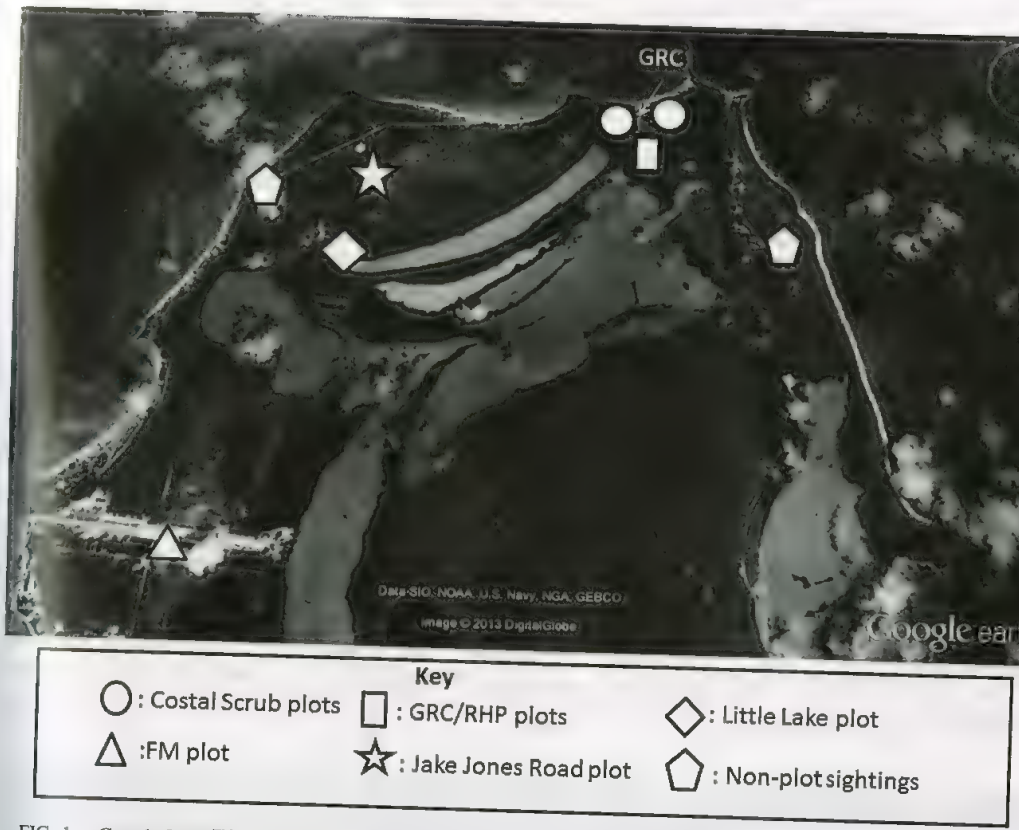

FIG. 1. Google Earth™ satellite imagery of the locations of study plots and other Kirtland's Warbler sightings on the northern half of San Salvador Island, The Bahamas.

female, based on plumage characteristics as described by Pyle (1997). Three additional individuals were also captured in the coastal scrub during the two field seasons, a second-year (SY) male on 1 March 2012 (Fig. 2), an ASY female on 10 March 2012, and a hatch-year (HY) female on 22 December 2012. Though the first and last individuals captured were never observed again, the other two individuals were re-captured on 14 and 11 March 2012, respectively. The male was re-captured 242 m from its original capture location, and the female was re-captured 99 m away.

In addition to capturing Kirtland's Warblers, we also had sixteen observations of foraging individuals on our study plots during the two study seasons. Most of these observations were relatively brief, with the observer sighting the bird long enough to identify it as a Kirtland's Warbler. We sighted individuals in coastal scrub habitat on 11, 17, 19, 20, 22, and 23 February 2012, and 9 and 27 February 2013 in the coastal scrub plots. Additionally, a bird was seen by another researcher on 1 October 2012 in one of our coastal scrub plots (K. Peiman, pers. comm.). We also sighted Kirtland's Warblers in inland low coppice on 23 February 2012 at the edge of a coastal scrub plot, 18 January, 7 February 2013 in Jake Jones Road, and observed birds on 23 February, 11 March, and 1 April 2013 in Little Lake.

We also observed Kirtland's Warblers while birding in other parts of the island outside of the study plots. One bird was sighted near "Fresh Lake" (24° 05′ N, 74° 26′ W) on 3 March 2013 and by "Triangle Pond" (24° 06′ N, 74° 31′ W) on 10 March 2013. The warblers were sighted in coastal scrub habitat and were also found to be foraging in *Erithalis fruticosa.*

We were able to confirm that most of the individuals were unbanded; however, two individuals were color-banded. The first individual, seen over a 40-sec observation period on 23 February 2012, was determined to have been originally

TABLE 1. Mist netting (12-m net hours), surveying (hours), and point count (hours) effort for different plots and years, on a study examining the wintering ecology of Prairie Warblers (*Setophaga discolor*) on San Salvador Island, The Bahamas.

January 2012–March 2012				
	Habitat types			
Effort types	Coastal scrub	GRC/RHP	Jake Jones/Little Lake	FM
Mist Netting	610	227	0	166
Surveying	75	1	0	33
Point Counts	4	0	0	5
December 2012–March 2013				
	Habitat types			
Effort types	Coastal scrub	GRC/RHP	Jake Jones/Little Lake	FM
Mist Netting	925	307	405	444
Surveying	106	20	51	48
Point Counts	1	0	1	1

captured in 2009 as a SY male near Mack Lake, Michigan, USA (S. Rockwell, pers. comm.). On 9 February 2013 we sighted another color-banded warbler, this time an even older individual originally captured as a SY male in the same area of Michigan in 2006 (S. Rockwell, pers. comm.).

Knowing that Kirtland's Warblers seldom travel more than 6 km during the non-breeding season (Wunderle et al. 2007), we conservatively estimate that we captured or sighted at least 10 individuals.

While capturing the individual on 11 March 2012 we observed a fecal sample that contained

FIG. 2. One of the Kirtland's Warblers, a second year (SY) male, captured in March 2012 on San Salvador Island, The Bahamas. Prior to the capture of this individual and several others, there had not been a confirmed sighting of a Kirtland's Warbler on the island since 1965. Photo by Todd Jones.

purple fruit. This is consistent with Wunderle et al. (2010) finding Kirtland's Warblers on Eleuthera frequently consuming fruit during the non-breeding season. Purple fruit-bearing plants occurred throughout the habitats where we encountered the birds. These included species such as *Erithalis fruticosa* and *Lantana involucrata*, whose fruits were frequently eaten by birds in Eleuthera (Wunderle et al. 2010). Presumably, the fruit from one of these plant species was what we observed in the fecal sample.

All of these observations occurred in coastal scrub and inland low-medium height coppice habitats. We did not capture or sight any birds within other sampled habitats in San Salvador, including tall coppice areas (>5 m in height), despite considerable search and mist-netting effort (Table 1). The coastal scrub and inland low coppice habitats on San Salvador are similar to Kirtland's Warbler wintering habitat described in other studies (Miller and Conroy 1990, Sykes and Clench 1998, Wunderle et al. 2010). These habitats generally have low vegetation (<4 m tall), a dense scrub/shrub appearance and usually have openings where the habitat has been disturbed, and contain fruit bearing plants. However, sightings in the Little Lake plot were an exception, where warblers were sighted in tree-like vegetation consisting of 4–5 m coppice. This habitat did have fruiting *Erithalis fruticosa*, suggesting that birds may also use slightly taller coppice if there is preferred fruiting vegetation.

Our observations of Kirtland's Warblers are, to our knowledge, the first documented sightings and captures on San Salvador Island in over 46 years (Haney et al. 1998). Despite surveys by birders, ornithologists, and student groups visiting the research center after 1970 (Miller 1978; Sordahl 1996; Murphy et al. 1998, 2001), it is possible that individuals were wintering on the island prior to our accounts, but were not detected for a number of reasons. The most likely being that previous surveys (Murphy et al. 1998, 2001) focused on habitat types such as stands of *Rhizophora mangle* and *Leucaena leucocephala* that appear to be less preferred by Kirtland's Warblers (Wunderle et al. 2010).

An alternative explanation for the gap in sightings of Kirtland's Warblers on San Salvador is that the species has actually been absent from the island for the past 46 years. Earlier sightings from the 1960s preceded observed declines in breeding populations in the 1970s (Probst et al. 2003) that could have caused the non-breeding range to contract as well. By this logic, the numerous encounters we report could be result of the species' recent population increase (Probst and Weinrich 1993, Kepler et al. 1996, Probst et al. 2003, fig. 2 in Donner et al. 2008) and breeding range expansion into Michigan's Upper Peninsula, Wisconsin, and Ontario (Probst et al. 2003, Richard 2008, Trick et al. 2008).

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Documentation of Predation of a Nestling Cerulean Warbler by a Red-bellied Woodpecker

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ABSTRACT.—Red-bellied Woodpeckers (*Melanerpes carolinus*) feed primarily on arthropods and plant matter, but a growing body of evidence suggests that Red-bellied Woodpeckers may also be a common passerine nest predator. Cerulean Warblers are the fastest declining Neotropical migratory wood warbler in North America. We report our observations of a Red-bellied Woodpecker depredating a nestling Cerulean Warbler (*Setophaga cerulea*) in Indiana. Further suggesting their status as a recognized nest predator, we also report agonistic behavior of a different Cerulean Warbler pair toward a Red-bellied Woodpecker foraging near the warblers' fledglings. Red-bellied Woodpeckers may be a more common nest predator of Cerulean Warblers than currently recognized, but further research is needed. *Received 3 October 2012. Accepted 15 January 2013.*

Key words: Cerulean Warbler, *Melanerpes carolinus*, mobbing, nest predation, predator, Red-bellied Woodpecker, *Setophaga cerulea*.

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The Red-bellied Woodpecker (*Melanerpes carolinus*) is a medium-sized woodpecker of the family Picidae whose range encompasses most of the eastern United States and extreme southern edge of Ontario (Shackelford et al. 2000). Populations of Red-bellied Woodpeckers, found in both mature hardwood forests as well as more urban settings, have increased across much of their range, particularly in the northeast (Sauer et al. 2011). They are known to feed mainly on plant matter and arthropods (Shackleford et al. 2000); however, there is increasing evidence that they also prey on songbird eggs and nestlings (Hazler et al. 2004). Hazler and others (2004) indicated that the woodpeckers may have a more substantial impact on the productivity of songbirds in many eastern North American forests than was previously recognized.

We report here the first detailed observations of a Red-bellied Woodpecker preying on a nestling Cerulean Warbler (*Setophaga cerulea*). Additionally, we describe agonistic behavior of a separate pair of Cerulean Warblers towards Red-bellied

FIG. 1. (A) Nest of Cerulean Warbler (*Setophaga cerulea*). (B) Red-bellied Woodpecker (*Melanerpes carolinus*) at nest of Cerulean Warbler prior to nestling removal. (C) Red-bellied Woodpecker probing the contents of the nest of Cerulean Warbler. (D) Red-bellied Woodpecker with nestling Cerulean Warbler in its bill.

Woodpeckers foraging near the warblers' fledglings. The Cerulean Warbler is a Nearctic-Neotropical wood warbler that breeds in mature deciduous forests of eastern and central North America. Populations of Cerulean Warblers have declined dramatically during the past few decades, and they are now listed as vulnerable to extinction by BirdLife International (2012) and endangered in Indiana (IDNR 2012). Understanding the causes of these declines is an important conservation mandate. Nest predation is likely an important cause of reproductive failure for this species (Boves and Buehler 2012), as it is for most passerine birds (Ricklefs 1969). However, a comprehensive study on Cerulean Warbler predation has not been conducted, and hence little is known regarding the diversity of nest predator species.

OBSERVATIONS

From May–July 2012, we regularly observed and filmed Cerulean Warblers feeding their young as part of a nestling diet study. On 1 June 2012, we observed and filmed parent Cerulean Warblers at a nest feeding a single nestling, approximately 6 days in age, during a routine 1-hr observation session in the Yellowwood State Forest, Brown County, Indiana (39° 06′ 31″ N, 86° 19′ 45″ W). This particular nest (Fig. 1A) was located ~18 m above the ground in a 28-m-tall white oak (*Quercus alba*). The nest was placed ~1.7 m away from the tree bole and ~2.4 m from the end of the branch. We observed the nest from 1409–1510 hrs EST and filmed the feedings using a Sony Cybershot 5× zoom attached to a Nikon Prostaff RAIII 82-mm spotting scope equipped with a 20–60× eyepiece. At 1423 hrs, a male Red-bellied Woodpecker landed on the nest branch <1 m away from the nest. Immediately, a parent Cerulean Warbler of unknown sex dove at the woodpecker in an agonistic manner but did not make contact. The woodpecker stayed on the branch for <1 min and subsequently flew off out of sight. It returned <5 secs later and landed on the trunk of the tree near the nest branch. After <5 secs, the woodpecker landed on the nest branch and hopped along the branch until it was at the nest (Fig. 1B). It stuck its head into the nest (Fig. 1C), pulled out a nestling (Fig. 1D), and

immediately flew out of our sight. We were unable to follow the woodpecker and consequently do not know whether it ate the nestling. We continued to observe and film the warbler parents and could hear loud alarm calls from the adults for at least 2 mins after the predation event. We continued to observe the nest until 1510 hrs, and observed the warbler pair return to the nest several times. During most of these visits, the warblers had food in their bill upon arrival and were observed to eat the prey themselves or fly away with it. We believe that the nestling that was removed was the last nestling in the brood based on the parents' post-predation behavior, and that this incident was the final cause of nest failure. Cerulean Warblers typically lay a clutch of 3–4 eggs (Hamel 2000). We lack knowledge pertaining to this particular pair's original brood size and whether it was greater than one, because we were unable to view the nest contents prior to the predation incident. A video of the predation event is available at: kislam.iweb.bsu.edu/Cerulean%20Warbler%20Research.htm

In addition to the predation event described above, we witnessed another pair of Cerulean Warblers, 1 km away from the predation event, exhibit agonistic behavior toward a Red-bellied Woodpecker that was near their fledglings. We first discovered the three fledglings within 8 m of their nest tree positioned on the ground or perched 1–2 m high in shrubs. Based on limited feather molt and inability to fly, these fledglings likely departed the nest on the day we first observed them (22 Jun). On 22 June at 1645 hrs, we saw a Red-bellied Woodpecker fly to a nearby snag ~8 m from a fledgling. Both the male and female Cerulean Warbler followed the woodpecker closely as it foraged on the snag. During ~4 mins of pursuit, the warblers chipped loudly but did not physically attack the woodpecker. Eventually, the woodpecker flew off and only then did the warblers resume feeding their young. On 24 June, two of the fledglings were relocated and a Red-bellied Woodpecker was observed foraging in a tree ~10 m from the fledglings. This time, only the male warbler followed the woodpecker as it foraged. The warbler remained about 2 m from the woodpecker, chipping loudly until the woodpecker flew away ~10 mins later.

DISCUSSION

Buehler and others (2008) considered Blue Jays (*Cyanocitta cristata*), American Crows (*Corvus brachyrhynchos*) and squirrels (*Sciurus* spp.) as potential nest predators of Cerulean Warblers in Indiana, Michigan, Mississippi, Tennessee, and Ontario, Canada; Boves and Buehler (2012) observed Blue Jays and eastern chipmunks (*Tamius striatus*) depredating Cerulean Warbler nests in Tennessee. However, scant research has been conducted to determine the importance of any one species or the full extent of predator diversity. Here, we provide direct evidence that Red-bellied Woodpeckers will depredate nests of Cerulean Warblers. Our observations of nestling predation, as well as agonistic behavior of parent Cerulean Warblers towards Red-bellied Woodpeckers in the vicinity of their fledglings, contribute to a growing body of evidence suggesting that Red-bellied Woodpeckers may potentially be important nest predators of many songbird species. Nestling predation of Cerulean Warblers by a Red-bellied Woodpecker has been reported on one other occasion in Tennessee (Beachy 2008). Red-bellied Woodpeckers have also been recorded depredating mostly single nests of the American Redstart (*Setophaga ruticilla*; Watt 1980), Acadian Flycatcher (*Empidonax virescens*; Trail 1991), Indigo Bunting (*Passerina cyanea*; Hazler et al. 2004), House Wren (*Troglodytes aedon*; Neill and Harper 1990), Blue-gray Gnatcatcher (*Polioptila caerulea*; Hazler et al. 2004), House Sparrow (*Passer domesticus*; Brackbill 1969), Carolina Chickadee (*Poecile carolinensis*; Conner 1974), White-breasted Nuthatch (*Sitta carolinensis*; Dunn 1984), and Tufted Titmouse (*Baeolophus bicolor*; Brown and Poole 2006). In addition to these confirmed records of predation events, observations of agonistic behaviors of other songbird species towards Red-bellied Woodpeckers suggest that the diversity of species affected by this nest predator may be even more widespread. Hazler and others (2004) documented Eastern Wood-Pewees (*Contopus virens*), Prothonotary Warblers (*Protonotaria citrea*), Blue-gray Gnatcatchers, and Acadian Flycatchers mobbing Red-bellied Woodpeckers when in close proximity to their nests. In these cases, mobbing occurred despite the apparent lack of interest in the nest by the woodpeckers.

In addition to Red-bellied Woodpeckers, several other woodpecker species have been described preying on the eggs and nestlings of songbirds. In North America, known predators include Red-headed (*Melanerpes erythrocephalus*; Smith et al. 2000), Acorn (*Melanerpes formicivorus*; Fajer et al. 1987), and Gila woodpeckers (*Melanerpes uropygialis*; Edwards

and Schnell 2000). A study in Sweden (Nilsson 1984) showed that woodpeckers (*Dendrocopos* spp.) were responsible for 17% and 48% of nest predation of tits (*Parus* spp.) in natural and artificial cavities, respectively. In Argentina, Magellanic Woodpeckers (*Campephilus magellanicus*) have been observed feeding their nestlings the eggs and nestlings of several other songbird species (Ojeda and Chazarreta 2006). While further study is needed, these observations suggest that woodpeckers in general may play a more important role as nest predators than previously recognized.

As populations of Cerulean Warblers have declined over the past 50 years in both Indiana and across the eastern United States (Sauer et al. 2011), Red-bellied Woodpecker populations have grown. From 2000–2010, populations of Red-bellied Woodpeckers increased by 3%/year in Indiana and nearly 2%/year across North America (Sauer et al. 2011). Thus, they may represent a growing pressure for the Cerulean Warbler and other canopy-nesting songbirds. To accurately determine the importance of Red-bellied Woodpeckers as nest predators of Cerulean Warblers and other canopy-nesting species, monitoring with 24-hour cameras will be required. A thorough investigation to document predators of Cerulean Warblers would be challenging, mostly because of the nest height. Additionally, predation studies generally require the use of expensive camera equipment, further limiting their feasibility. However, knowledge of nest predator diversity would be useful to our understanding of the causes of population declines of Cerulean Warblers.

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Responses of Common Tern Chicks to Feather Sample Removal

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ABSTRACT.—Feather sampling is often assumed to be harmless, but this assumption has not been tested. From 2008–2012, we recorded the behavior of 340 Common Tern (*Sterna hirundo*) chicks following the removal of a pinch of body feathers. Only 11.2% of these chicks ran after sampling and 69.4% showed no visible reaction to sampling. The probability of a chick running away increased with age. We therefore recommend that sampling be conducted as soon as possible after juvenal feathers emerge. There was evidence for individual differences in behavior: approximately 71% of chicks that ran after feather sampling also ran away when re-encountered on later dates, while other chicks rarely did so. We found no evidence that removal of feather samples increased chick mortality, supporting the assumption that this technique is minimally invasive, but small differences in mortality rates would have been difficult to detect. *Received 3 January 2013. Accepted 7 April 2013.*

Key words: Common Tern, feather samples, investigator disturbance, semi-precocial, *Sterna hirundo*.

Feather samples taken from live birds have a variety of uses. Feathers can provide DNA for genetic studies and molecular sexing, and can provide material for stable isotope studies of feeding ecology, measuring levels of contaminants, ptilochronology, hormonal studies, and color analyses (e.g., Grubb 1989, Taberlet and Bouvet 1991, Burger 1993, Becker et al. 2002, Siefferman and Hill 2003, Smith et al. 2003, Harvey et al. 2006, Bortolotti et al. 2008, García-Fernández et al. 2013). Although samples can be gathered noninvasively if using shed feathers (Rudnick et al. 2007), feathers often need to be removed from live birds in the hand.

Although blood samples provide more live tissue than feather samples, feather sampling has several advantages over blood sampling (but see McDonald and Griffith 2011 below). Collecting feather samples requires little training, requires less handling time than removing blood, and produces no hazardous waste (Harvey et al. 2006). It is also easier to get permission to take feather samples. With one notable exception (Brown and Brown 2009), most previous studies have found no adverse effects from blood sampling (Redmond and Murphy 2011 and references therein), and it has been commonly assumed that removal of a small number of feathers also has little effect on birds.

However, McDonald and Griffith (2011) suggest that feather sampling is likely to be harmful. For example, there may be physiological costs associated with altered thermoregulation and production of replacement feathers, the removal of flight feathers may affect flight performance, and the low yield of DNA provided by feathers may require repeated sampling. The impact of feather sampling has not previously been tested on wild birds. The only relevant papers we could locate demonstrate no physiological effects, except those induced simply by handling stress, of harvesting feathers from molting domestic geese (*Anser anser domesticus*; e.g., Tóth et al. 2012).

Even if no direct effect of feather sampling occurs, it is possible that indirect negative effects may occur through changes in behavior. For example, Common Terns (*Sterna hirundo*) nest colonially and have semi-precocial chicks. Com-

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mon Tern chicks often run away from investigators after handling (Gochfeld 1981). Although they usually return near the nest, chicks that run risk becoming separated from parents and risk potentially lethal aggression from other adults (Gochfeld 1981, Quinn et al. 1994, Palestis and Burger 2001b). Feather samples from Common Tern chicks (and adults) have been used by previous authors, most frequently for biomonitoring of mercury contamination (Becker et al. 1993, 1994; Burger and Gochfeld 1997; Nisbet et al. 2002).

We recorded the reactions of Common Tern chicks to the removal of a pinch of juvenal body feathers from the side and examined factors that could lead to variation in the responses of individual chicks. Based on Gochfeld's (1981) study of the responses of Common Tern chicks to handling, we predicted that the frequency of running and/or distance run should increase with chick age, with intensity of handling, and on cloudy days.

METHODS

This study was performed from 2008–2012 at Pettit Island, a small saltmarsh island in Barnegat Bay (39° 40′ N, 74° 11′ W, New Jersey, USA). The number of Common Tern breeding pairs at this site varied from approximately 125–300 across years. The median nearest neighbor distance among nests has been measured as 1.04 m on mats of eelgrass (*Zostera* sp.) and other dead vegetation, the most common nesting substrate, and 1.90 m among nests in *Spartina alterniflora* (Palestis and Burger 2001a). We took feather samples from 340 chicks over 5 years. Field work was performed under BGP's state scientific collecting permits and federal bird-banding permit.

Most chicks in the colony were banded when still in or near the nest and when too young for feather sampling. When chicks were at least 1 week old with pin feathers or more developed juvenal feathers present on the body, small numbers of feathers were removed and placed in labeled envelopes. Samples were not taken from the same chick twice. Chicks were typically hiding in vegetation when feather sampling occurred. As recommended by Gochfeld (1981), to reduce the tendency for chicks to run after handling, chicks were not picked up unless absolutely necessary and therefore remained in their hiding places after sampling. A feather sample can be taken without picking up the chick, simply by holding back a wing and grabbing a pinch of feathers from the side. In addition, after handling, a hand was placed over each chick for a few seconds before release.

Any immediate response of a chick to removal of feathers was recorded. We then recorded whether the chick ran after handling. Distance run was measured to the nearest 0.1 m in half of the cases (19 of 38). If the chick moved farther in response to us approaching the chick again to measure distance, the additional distance was not included. We compared the chicks by age (<2 wks, >2 wks, or >3 wks), handling intensity (feathers only or feathers together with banding), and weather (sunny, cloudy, intermediate). We also recorded whether a chick ran during subsequent encounters, whether fleeing to evade capture or running after we checked the band number.

We focused on chick behavior and do not have detailed information on survivorship. However, counts of dead chicks should indicate if mortality is relatively higher among feather sampled chicks than among non-sampled chicks. When comparing mortality between sampled and control chicks, we include data only from 2008 and 2009, when field work focused more on chicks than in other years and censuses were more frequent. The inclusion of additional years would not change the conclusion, but we have less confidence in the data from other years. We exclude any deaths recorded in the first week of life, when mortality rates are highest but chicks are still too young for feather sampling.

RESULTS AND DISCUSSION

Of 340 chicks, 236 showed no visible reaction to feather removal (69.4%). Only 38 chicks ran after feather removal (11.2%). Other reactions included changing position, calling, and biting. The frequency of running varied little among years, ranging from approximately 9–13.5% of chicks, and years are combined in the analyses below.

Older chicks ran more frequently than younger chicks (Table 1). The frequency of running was very similar in chicks between 2–3 weeks old and those older than 3 weeks. Because relatively few chicks older than 3 weeks were sampled (Table 1), in all statistical analyses these two categories were combined, thus all comparisons are between chicks older than and younger than two weeks. The frequency of running also

TABLE 1. Frequency of chicks running after feather sample removal, divided by age in weeks, handling intensity (feather sampling alone or feather sampling simultaneous with banding), and weather (cloud cover). Total sample size n is smaller for age (n = 300) than other variables (n = 340), because chicks at the border between weeks or of undetermined age were excluded.

Variable		Percent that ran	n
Age	<2 weeks	6.9	173
	All chicks >2 weeks	18.9	127
	>2 weeks but <3 weeks	18.8	96
	>3 weeks	19.3	31
Handling	Feathers only	10.6	246
	Feathers + banding	12.8	94
Weather	Sunny	9.7	207
	Intermediate	12.0	50
	Cloudy	14.5	83

appeared slightly higher among chicks banded at the same time feathers were removed and increased on cloudy days (Table 1). In the worst case scenario (>2 wks, band + feathers, and cloudy), 5 of 14 chicks ran (36%), compared to 6% (n = 103) in the best case scenario.

A logistic regression with the dependent variable as whether a chick ran showed that only the age effect was statistically significant (odds ratio = 3.55, Wald P = 0.027; overall regression Nagelkerke r^2 = 0.10). The effect of cloud cover was marginal (odds ratio = 1.75, Wald P = 0.085) and there was no significant effect of additional handling (odds ratio = 0.40, Wald P = 0.39). There were also no significant interaction effects (all $P > 0.10$).

Distance run averaged 1.9 m and was highly variable (SD = 1.4 m). None of the variables significantly affected distance run (General Linear Models with and without interactions, all $P >$ 0.10), but sample size is small for distance run and distance is underestimated for older chicks which occasionally ran to water (n = 5). Based on the typical distance between nests at this site (see Methods), chicks often entered neighboring territories when running after feather sampling. It is likely that distance run in this saltmarsh colony is shorter than it would be in more open habitat. Common Tern chicks on sandy beaches run much more frequently and much farther in response to handling (touching, banding, or picking up) than the numbers reported here, and they run to reach vegetation (Gochfeld 1981).

Chicks that ran after feather sampling often ran again when re-encountered on later dates (15 of 21 chicks, 71.4%), while other chicks rarely did so (<5% of chicks). This result suggests either individual differences in the tendency to run, or that the experience of running from a "predator" increases the likelihood of running in future encounters.

Taking feather samples did not appear to increase mortality, judging by counts of dead chicks in 2008 and 2009 (excluding those killed in a major flood in 2009). Only four of 170 chicks that had feather samples removed were later found dead (2.4%). This frequency is very similar to that for control chicks: five of 136 (3.7%) found dead (2 × 2 Contingency Chi-Square with Yates' Correction: χ^2_1 = 0.12, P = 0.73). None of the chicks that ran following feather sampling were later found dead in any year of the study.

Feather sample removal appears to be minimally invasive, as most chicks did not run and no adverse effects of feather sample removal were observed. We rarely banded chicks old enough for feather sampling without also taking feathers, but the observations we have suggest that the frequency of running after banding alone (10.0%, n = 30) is similar to that for feather sampling alone (10.6%, Table 1). The responses to feather sampling may therefore reflect a more general response to handling than a response to feather removal per se. Although we did not detect any effects of feather sampling on mortality, survival to fledging was not tracked intensively and subtle effects on chick survival could have been overlooked. Chick survival is particularly difficult to estimate accurately in a species in which chicks move away from the nest site and hide from investigators (Erwin and Custer 1982, Nisbet et al. 1990). Chicks that did run often fled through neighboring territories, thus it is surprising that no runners were found dead (Quinn et al. 1994,

Palestis and Burger 2001b). Zingo (1998) found no adverse effects of repeated handling (e.g., regular weighing) on Roseate Tern (*S. dougallii*) chicks, but the chicks did not flee after handling. On the other hand, Black Skimmer (*Rynchops niger*) chicks run farther and more frequently than Common Terns (Gochfeld 1981), and there is likely to be considerable variation among species in responses to feather sampling.

Because running by semi-precocial chicks in a dense colony has the potential to cause harm, we recommend a cautious approach. It is probably best to take feather samples as soon as possible after juvenal feathers emerge, when chicks are relatively young and running is less likely. It is also possible that sampling from chicks close to fledging is safe, because these highly mobile chicks are no longer tied to a nest site. It may also be best to avoid or limit sampling on cloudy days. Furthermore, fence erection around study nests would decrease the distance that chicks can run after feather sampling or other types of handling. Such enclosures are usually safe, but can also cause harm, depending on the species, habitat type and construction material (Erwin and Custer 1982, Nisbet et al. 1990, Eyler et al. 1999).

Terns tend to tolerate repeated intrusion into colonies and handling by careful investigators (Nisbet 2000), and with simple precautions feathers can be collected from chicks with little effect on the birds. However, we have studied only one species in one habitat type, and removed only juvenal body feathers. Other species may be more sensitive to feather sampling, and the effects of feather sampling may also vary with age class, feather type, time of year, and habitat. Additional studies of the effects of feather sampling are therefore clearly needed (McDonald and Griffith 2011).

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Agonistic Interactions in Raptors of the Pampas Region

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ABSTRACT.—In this study, we evaluated the interspecific agonistic responses of raptors and non-raptors, elicited by the presence of five raptor species (*Circus cinereus*, *C. buffoni*, *Rupornis magnirostris*, *Elanus leucurus*, and *Geranoaetus melanoleucus*) in the Pampas region of Argentina. We registered 62 agonistic interaction events, most of them involving two raptor species (58%). During these events we registered 122 attacks, 10 persecutions, and three cases of kleptoparasitism. *Milvago chimango* was the most important aggressor species among raptors, and *Vanellus chilensis* among non-raptor birds. Attacks in groups were more frequently performed by non-raptors (61.5% of the events involved two or more aggressor individuals) than by raptors (68.5% of the events involved only one aggressor). This study represents a primary approach to one scarcely explored aspect of raptor behavior in southern South America. *Received 20 November 2012. Accepted 7 April 2013.*

Key words: aggressive behavior, Argentina, body size, diurnal raptors, dominance hierarchy.

Agonistic interactions among birds occur when the interests of two or more individuals are in conflict. Among Falconiformes these interactions are usually related to the defense of hunting or breeding territories (Newton 1979). Such behaviors may be relatively non aggressive (e.g., posturing, flight displays; Jamieson and Seymour 1983), aggressive (e.g., persecutions, escorting flights, attacks; Bildstein and Collopy 1985), or a combination of both (Dawson and Mannan 1991). Since raptors are potential predators of nests and fledglings, agonistic interactions often involve not only other raptors, but also smaller non-raptors (Vasina and Straneck 1984, Saggese and De Lucca 2001, De Lucca 2011). Body size seems to be an important factor in determining agonistic behavior. Large-sized raptors tend to elicit more aggressive reactions than do smaller ones (Jiménez and Jaksic 1989, Liébana et al. 2009), which may be related to dominance hierarchies (large individuals are usually dominant over small ones; Yahner 2012). Individuals of smaller size species tend to associate during agonistic interactions in an attempt to disable or drive large predators from the vicinity of their nesting sites (Desrochers et al. 2002, Arnold et al. 2005).

In the southern cone of South America studies about agonistic interactions in raptors are scarce and, in most cases, they report information in relation to the reproductive behavior (Saggese and De Lucca 1995, 2001; De Lucca and Saggese

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1996; Baladrón et al. 2006; Salvador-Jr. et al. 2008; Liébana et al. 2009; but see Jiménez and Jaksic 1989; De Lucca 2011). In this study, we describe the interspecific agonistic interactions of sympatric raptor and non-raptor species in the Pampas of Argentina, in order to evaluate relationships between the occurrence of this behavior and characteristics of the species involved. We expect to find that if body size is a key factor in determining agonistic behavior of birds in the study area: (1) the intensity of interactions should increase along with the size of the potential predator, and (2) small birds should display associative behavior to repel large raptors.

From 2005–2008, we documented the agonistic interactions of diurnal raptors in Mar Chiquita County, southeast Buenos Aires Province, Argentina (37° 32′–37° 45′ S; 57° 19′–57° 26′ W). The sampling was conducted in an opportunistic manner throughout the period (including reproductive and non reproductive seasons), as part of a broader project aimed to register the activity patterns of raptors that inhabit the study area. The area is located in the Pampas region and includes zones of native vegetation including marshes and grasslands, and zones of agriculturally-modified environments (mainly pasturelands) (Isacch 2008). We registered the response of raptors and non-raptors to the presence of five species of raptors (hereafter, target species): Cinereous Harrier (*Circus cinereus*), Long-winged Harrier (*C. buffoni*), Roadside Hawk (*Rupornis magnirostris*), White-tailed Kite (*Elanus leucurus*) and the Black-chested Buzzard-Eagle (*Geranoaetus melanoleucus*). All these species are mainly carnivorous, and show different abundances (AVB, unpubl. data), hunting modes (Bó et al. 2007), and body sizes (Ferguson-Lees and Christie 2001). The Cinereous and the Long-winged harriers are medium-sized raptors (~420 g and ~500 g, respectively), the first is considered as rare and the second as occasional; both harriers are active-search bird-eating predators (Baladrón et al. 2012). The Roadside Hawk is a medium-sized raptor (~315 g), whose abundance has increased in recent years at the study area (see Baladrón et al. 2011). The White-tailed Kite is a common small-medium raptor (~280 g) with a diet composed mainly of small mammals which are captured by hovering (Dunk 1995). The Black-chested Buzzard-Eagle is the biggest raptor of the target group (~2200 g) and is quite rare in the study area.

During each interaction event we registered the aggressor and target species, the number of individuals involved, the number and type of interaction (i.e., attacks: when the aggressor attempts to contact other individual using the bill or talons; kleptoparasitism: when the aggressor steals food from other individual; persecutions: when the aggressor expulses other individual from the area [without attacking]). In addition, we recorded the activity performed by target species during each interaction event (i.e., flying, feeding, perching, foraging [sit-and-wait or active search], and nest defense).

During the study period, the five target species elicited a total of 62 agonistic interaction events, most of them with other raptor species (58%), and the remaining with non-raptor species (Table 1). During these events, we registered 122 attacks, 10 persecutions, and three cases of kleptoparasitism. The Black-chested Buzzard-Eagle, the largest raptor of the target group, was the species that elicited more attack responses from other birds (28.7% of total attacks). The remaining interaction events were elicited mainly by the Long-winged Harrier and the Roadside Hawk (27% and 25.4%, respectively), and by the Cinereous Harrier (11.5%) and the White-tailed Kite (7.4%) (Table 1). The 50% of events involved the Chimango Caracara (*Milvago chimango*) and the Southern Caracara (*Caracara plancus*) as aggressor species.

Our results show that body size was important in determining agonistic responses, since more than 95% of the events involved a smaller bird harassing a larger one. The importance of body size may be related to the dominance hierarchy (Martínez et al. 2008, Yahner 2012), which entails that larger species are more often harassed by smaller ones (Jiménez and Jaksic 1989). Similar results have been observed for the Peregrine Falcon (*Falco peregrinus*), which frequently attack larger raptors (e.g., Southern Caracaras) but do not attack smaller ones (e.g., American Kestrel [*Falco sparverius*], White-tailed Kite, and Chimango Caracara) in central Argentina (Vasina and Straneck 1984). No relationship was evident between the frequency of attacks and the relative abundance of the target species, which may indicate that body size is more important than abundance in determining agonistic behavior.

Among raptors, the Chimango Caracara appeared as the most important species in stimulating interspecific agonistic interactions. This

TABLE 1. Agonistic interaction events between the five target raptor species and other raptors and non-raptors in the southeastern Pampas of Argentina. Numbers indicate the sum of cases we registered for each type of interaction (attack-kleptoparasitism-persecution). n.d.: no data.

Aggressor species				Target species				
Common name	Scientific name	Mean weight (g)	*n* individuals	Roadside Hawk	Black-chested Buzzard-Eagle	Long-winged Harrier	Cinereous Harrier	White-tailed Kite
Raptors								
Chimango Caracara	*Milvago chimango*	295	1	4-0-0	–	1-2-0	4-0-0	3-1-3
			2	–	3-0-0	–	–	–
			3	–	–	4-0-0	0-0-1	–
			5	–	–	–	4-0-0	–
			8	–	–	–	2-0-0	–
			14	–	–	–	0-0-1	–
Southern Caracara	*Caracara plancus*	1,380	1	–	1-0-0	–	–	3-0-5
			3	–	1-0-0	–	–	–
			4	–	3-0-0	–	–	–
			5	–	5-0-0	–	–	–
American Kestrel	*Falco sparverius*	117	1	23-0-0	–	–	–	–
Non-raptors								
Southern Lapwing	*Vanellus chilensis*	310	1	–	–	5-0-0	–	–
			2	–	3-0-0	4-0-0	–	–
			3	–	2-0-0	5-0-0	–	–
			4	–	–	2-0-0	–	–
			5	–	16-0-0	–	–	–
Unidentified passerines		n.d.	1	–	–	–	3-0-0	2-0-0
			2	–	–	2-0-0	–	–
Brown-and-yellow Marshbird	*Pseudoleistes virescens*	75	1	–	–	2-0-0	–	–
			3	–	–	8-0-0	–	–
Great Kiskadee	*Pitangus sulphuratus*	70	1	1-0-0	–	–	–	–
Chalk-browed Mockingbird	*Mimus saturninus*	74	1	3-0-0	–	–	–	1-0-0
swallows		20	3	–	–	–	1-0-0	–
			20	–	–	–	–	–
Monk Parakeet	*Myiopsitta monachus*	124	45	–	1-0-0	–	–	–
Total Interactions				31-0-0	35-0-0	33-2-0	14-0-2	9-1-8

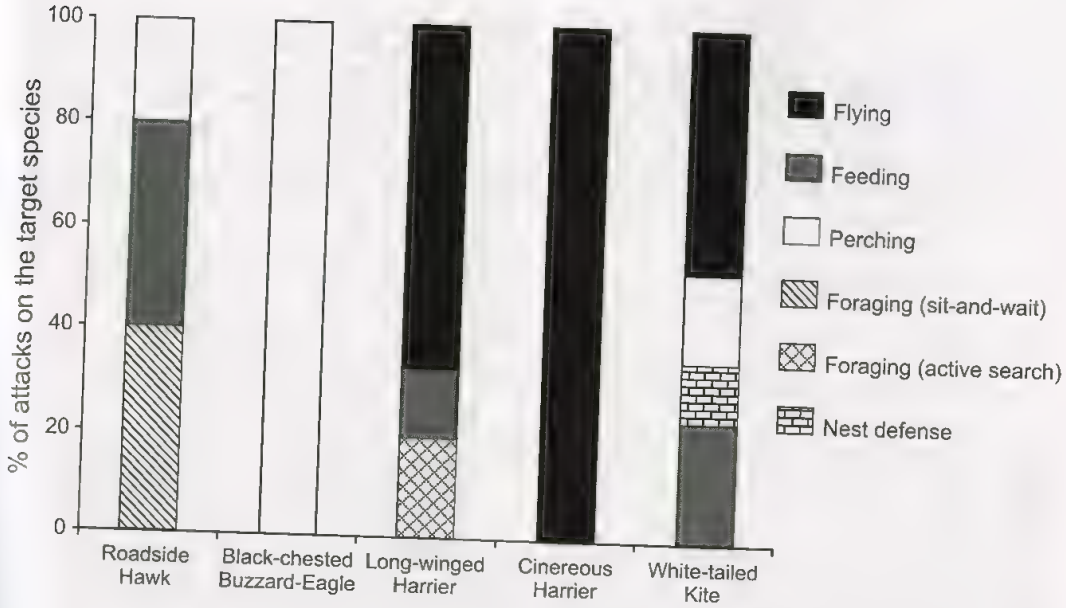

FIG. 1. Frequency of attacks on the target species for each activity type.

species performed the highest percentage of the total attacks (41%; Table 1), and was the only species that interacted with the five target species; it was also the most common receiver of interactions (see below). The Chimango Caracara shows the highest population density among raptors in the Pampas region (Ferguson-Lees and Christie 2001, Martínez 2001). Although the participation of this species is related to its abundance in the study area, we believe that it is also enhanced by the intrinsic behavioral traits of this raptor. For instance, it has been reported that this raptor may use alternative mechanisms to obtain food, such as kleptoparasitism (García and Biondi 2011) or mutualistic associations with larger raptors (Baladrón et al. 2009), which may be associated to agonistic behavior. Among non-raptors, the Southern Lapwing (*Vanellus chilensis*) was the most aggressive species, accounting for 60.7% of the total attacks on the target species (Table 1). The aggressive behavior of this species has been extensively reported (Saggese and De Lucca 2001, Baladrón et al. 2006, De Lucca 2011) and is related to the intensive efforts to keep intruders away from the nesting site.

Among non-raptors, most of the events (61.5%) involved two or more aggressor individuals (Table 1). This associative behavior, or mobbing, is a typical defense behavior of many gregarious species (Arnold et al. 2005). This may be the case of the Brown-and-yellow Marshbird (*Pseudoleistes virescens*), which performed 43.5% of the attacks among passerines. This is a gregarious species that shows cooperative breeding (Mermoz and Reboreda 1998), and it is probable that the helpers participate in predator mobbing (Arnold et al. 2005). In contrast among raptors, most cases included one-by-one interactions (68.5% of the events; Table 1).

The activity type displayed by the target raptors showed low incidence on the generation of agonistic responses. For instance, the Black-chested Buzzard-Eagle and the Roadside Hawk were attacked while perching (i.e., searching for prey, feeding or resting); whereas, harriers were attacked mostly in flight (i.e., during cruising flights or searching for prey) (Fig. 1). In this sense, the frequency of attacks by activity type seemed to relate to the typical activity patterns of each species of the target group (Bó et al. 2007).

In addition, we registered 15 cases of reverse interaction (i.e., when target species harassed other birds), all of them involving two individual raptors. These events included persecutions (n = 11) and attacks (n = 4). The most frequent aggressor species was the White-tailed Kite (73.3% of the events), followed by the Cinereous

Harrier (20%), and the Long-winged Harrier (6.7%). The Chimango Caracara was the most common recipient of reverse interactions (53.3% of the events), followed by the Southern Caracara (46.7%). It is important to note that all cases of reverse interactions performed by target species were in response to previous attacks of the other bird, as a mode of nest defense, or to avoid food piracy.

Our study represents a primary approach to one rarely explored aspect of raptor behavior in southern South America. Although the number of observations and the nature of data constrain the scope of our work, our findings contribute to a more complete understanding of the relationships among sympatric raptor and non-raptor birds.

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Winter Diet of Long-eared Owl *Asio otus* in a Mediterranean Fragmented Farmland

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ABSTRACT.—The Long-eared Owl (*Asio otus*) is a widely distributed predator with plastic foraging habits. Its diet has been studied across most of Europe and North America, but little information is available on intra-seasonal diet variation. We studied the winter diet of Long-eared Owls in a Mediterranean fragmented farmland. Diet was dominated by small mammals (mostly *Apodemus* spp.), with birds the second most abundant group. In our landscape, the amount of bird prey items in the diet was higher compared to values reported from other areas of Italy. There was relatively large variation in the diet among the three months of study. Our study confirms the pattern of higher Long-eared Owl diet diversity in a Mediterranean landscape compared to that reported for other regions of Europe where the diversity of prey species may be lower. The findings suggest that extensively-managed Mediterranean rural landscapes can provide habitat suitable for the Long-eared Owl, as they offer a wide diversity of food sources that may be exploited by this nocturnal predator. *Received 8 January 2013. Accepted 20 March 2013.*

Key words: feeding ecology, food niche, foraging behavior, pellet analysis, rural habitat, small-mammal.

The Long-eared Owl (*Asio otus*) is commonly considered a small mammal (specifically vole)-eating specialist (Marti 1976, Romanowski and Zmihorski 2008), with mice the dominant prey only in limited areas of Europe (Marti 1976). Its feeding behavior is known to vary according to different conditions, such as landscape and climatic zone (Marti 1976) but also among different seasons within a year (e.g., Tome 1994). Studies carried out in southern Europe (see Bertolino et al. 2001 and references therein) have shown that the diet of Long-eared Owls is generally based on at least three main prey groups and differs from that from central and northern Europe, where voles are the dominant prey. An analysis of pellets from northern Italy (Bertolino et al. 2001) has shown that these birds are opportunistic predators able to expand their food niche in the presence of diversified prey. The diet of Long-eared Owls is well studied in North America and in northern and central Europe (Marti 1976, Birrer 2009), but fewer studies have addressed this topic in the Mediterranean landscape (here referring to the Mediterranean biome with typical climate and vegetation bordering the Mediterranean sea; but see e.g., Capizzi et al. 1998, Birrer 2009, Charter et al.2012).

METHODS

In this study we analysed the diet of Long-eared Owls wintering in a typical Mediterranean rural landscape (Castel di Guido farm, 8 km west of Rome: 41°52′N, 12°17′E) characterized by cultivated fields (*Triticum* sp. and *Medicago sativa*), large pastures (grazed by cows and sheep) and woodland patches, both natural (mainly *Quercus ilex* and *Q. pubescens*) and artificial (mainly pine and oak plantations).

A Long-eared Owl roosting site was discovered in late November 2002 in a pine plantation. The site was fully cleared of all pellet remains 10 days before the first collection date. Pellet collection started on 9 December 2002 and finished at the end of February 2003, when only few individuals were still present at the roost. Samples were

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TABLE 1. Diet parameters of Long-eared Owls wintering in Castel di Guido farm (Rome, Italy): number of items collected every 10 days of each month (I–II–III); monthly frequency of occurrence (F. tot%) and biomass (B. tot%) of each item are shown, along with numbers for the overall winter (two rightmost columns: frequency of occurrence F. TOT% and biomass B.TOT%). Biomass values for each taxon (B.) were obtained from small-mammal trapping projects carried out in Castel di Guido, with the exception of values within brackets which were extracted from other sources (see main text for details). The total number of collected and analyzed items, as well as the total number of owls detected at the roost at each sampling session are also reported in the bottom of the table (last three rows).

		DECEMBER					JANUARY					FEBRUARY						
TAXON	B. (g)	I	II	III	F. tot %	B tot %	I	II	III	F. tot %	B. tot %	I	II	III	F. tot %	B. tot %	F TOT %	B.TOT %
Suncus etruscus	(2.5)	*0*	*0*	*1*	0.29	0.03	*0*	*0*	*0*	0	0.00	*0*	*0*	*0*	0	0.00	0.09	0.01
Crocidura sp.	5.42	*1*	*1*	*0*	0.58	0.13	*0*	*0*	*1*	0.25	0.06	*1*	*0*	*0*	0.29	0.06	0.36	0.08
Crocidura leucodon	6.4	*0*	*1*	*0*	0.29	0.08	*0*	*0*	*0*	0	0.00	*0*	*0*	*0*	0	0.00	0.09	0.02
Apodemus sp.	27.82	*28*	*24*	*13*	18.79	22.06	*20*	*30*	*28*	19.12	23.05	*22*	*18*	*8*	13.79	15.21	17.33	20.14
Mus domesticus	11.11	*8*	*17*	*12*	10.69	5.02	*20*	*12*	*18*	12.25	5.90	*16*	*17*	*17*	14.37	6.33	12.43	5.77
Muridae undet.	19.47	*22*	*16*	*19*	16.47	13.54	*33*	*16*	*23*	17.65	14.89	*9*	*18*	*13*	11.49	8.87	15.34	12.47
Rattus rattus	(120)	*4*	*2*	*5*	3.18	16.11	*0*	*4*	*4*	1.96	10.20	*4*	*5*	*1*	2.87	13.67	2.63	13.19
Rattus sp.	(135)	*0*	*0*	*1*	0.29	1.65	*1*	*2*	*0*	0.74	4.30	*3*	*3*	*2*	2.3	12.31	1.09	6.14
Microtus savii	(20)	*18*	*18*	*15*	14.74	12.44	*25*	*33*	*34*	22.55	19.55	*24*	*22*	*22*	19.54	15.50	19.15	15.99
Microtidae indet.	(20)	2	*0*	2	1.16	0.98	*4*	*0*	*11*	3.68	3.19	*9*	*4*	*8*	6.03	4.79	3.63	3.03
Clethrionoyms glareolus	(29.5)	*1*	*0*	*0*	0.29	0.36	*0*	*0*	*1*	0.25	0.31	*1*	*0*	*0*	0.29	0.34	0.27	0.34
Muscardinus avellanarius	18.11	*2*	*4*	*3*	2.60	1.99	*2*	*3*	*0*	1.23	0.96	*1*	*3*	*0*	1.15	0.83	1.63	1.24
Aves	(20)	*45*	*33*	*24*	29.48	24.89	*15*	*19*	*48*	20.1	17.42	*27*	*43*	*27*	27.87	22.10	25.5	21.30
TOTAL ITEMS		131	116	95	346		120	119	168	408		117	133	98	348		1,102	
ANALYZED PELLETS		124	104	84	312		93	100	101	294		100	100	100	300		906	
COUNTED OWLS		8	>10	17			20	18	19			13	9	4				

collected at 10-day intervals. As in previous studies, during the pellet analyses, bird remains were pooled into a single group and mammals were identified at the species level when possible, with the exception of bats (Galeotti and Canova 1994, Riga and Capizzi 1999). The diet of the Long-eared Owls was characterized using percentage of occurrence of each item and biomass. Biomass values for each taxonomic category were obtained from small-mammal trapping projects carried out in Castel di Guido and complemented with previously published data (Riga and Capizzi 1999, Pirovano et al. 2000) when taxonomic groups were lacking from the trapping effort.

RESULTS

We identified a total of 1,102 prey items from 906 pellets. Small mammals (*Soricomorfes* and *Rodentia*) contributed the most in terms of prey items by number and biomass (74% and 78.4%, respectively), followed by birds (24.5% and 21.3%). Among the small mammals, *Apodemus* sp. was the main prey in number and biomass (both *A. sylvaticus* and *A. flavicollis* are present in the study area; Imperio et al. 2007), closely followed by *Microtus savii* (Table 1).

Diet composition, analysed only considering the four main prey categories in number (those constituting at least 5% of prey items over the entire season; Pirovano et al. 2000) and excluding "*Muridae indeterminate*" (Table 1), varied significantly between months ($\chi^2 = 19.13$, df = 6, $P = 0.004$). This result confirms that Long-eared Owls may switch between different prey groups within the same season. This finding was previously reported only in a few studies, mostly in urban environments of northern Italy (e.g., Pirovano et al. 2000; Rubolini et al. 2003; but see also, e.g., Tome 2009). In December, *Apodemus* and birds were the dominant prey categories in terms of biomass. In January, the contribution of birds in the pellets' biomass decreased, while that of *Apodemus* remained stable and that of *M. savii* increased. In February, birds again returned to be dominant in terms of biomass, followed by *Apodemus*. Values for *Mus* seem to be stable through the sampled period (Table 1). *Soricomorfes* species and bats represent a very small fraction of the pellets' biomass, as well as *Clethrionoyms glareolus*. The latter values are probably explained by the low presence of the species in the area, while *Soricomorfes* species are known to be a less favored prey (Korpimäki and Norrdahl 1989, Birrer 2009). The low consumption of bats is common in areas where sites of bat aggregation are absent (García et al. 2005). Despite the abundance of *Muscardinus avellanarius* in the study area (Imperio et al. 2007), the species was rarely present in the analyzed pellets, probably because of its arboreal habits which make it less available to an open-land predator like the Long-eared Owl. *Rattus* species were found in small numbers but their contribution in biomass was relatively large (Table 1). Invertebrates and amphibians were absent in the diet because the sampling period was concentrated in winter when these taxonomic groups are rarely available.

DISCUSSION

The diet composition of Long-eared Owls wintering in the farmland landscape was rather diverse. It was based on four main item groups in number of prey and five groups in biomass (Table 1). This represents a major diversification in diet composition compared to that reported from other areas of Europe (Birrer 2009). Even though the presence of birds is well known in the diet (Marti 1976, Birrer 2009), it was surprising to find the large contribution this prey group made to the overall diet of the owls in our local area compared to that recorded in other localities (e.g., Riga and Capizzi 1999). This occurrence is likely a result of both hunting behavior of the species at dusk and the abundance of this food source in the area.

Overall, the results of the present study are consistent with previous findings (Bertolino et al. 2001, Rubolini et al. 2003), suggesting that the Long-eared Owls are flexible predators in terms of their diet. The study also highlights the rapid change in diet composition within the same season, probably as a consequence of changes in prey availability in the environment. This aspect has been largely overlooked by previous studies. Our findings also suggest that extensively-managed Mediterranean rural landscapes can provide habitat that can be used by wintering Long-eared Owls owing to the wide diversity of food sources that may be exploited by this nocturnal predator.

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The Relationship of Blue Crab Abundance to Winter Mortality of Whooping Cranes

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ABSTRACT.—We sampled blue crab (*Callinectes sapidus*) numbers in marshes on the Aransas National Wildlife Refuge, Texas from 1998–2006, while simultaneously censusing the wintering population of Whooping Cranes (*Grus americana*) on the refuge and surrounding habitats. This was done to determine whether mortality of wintering Whooping Cranes was related to the availability of this food source. Yearly variation in crab numbers was high, ranging from a low of 0.1 crabs to a high of 3.4 crabs per 100-m transect section. Significant non-linear increases in both juvenile and adult mortality in relation to decreasing crab abundance was observed. Results suggest that some threshold of crab abundance exists in which Whooping Cranes have higher survival on their wintering grounds.
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Key words: Aransas-Matagorda National Wildlife Refuge, blue crab, *Callinectes sapidus*, feeding ecology, *Grus Americana*, mortality, Whooping Crane.

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Blue crabs (*Callinectes sapidus*) are an important food source for the endangered migratory Aransas-Wood Buffalo population of Whooping Cranes (*Grus americana*) while wintering at the

Aransas National Wildlife Refuge (NWR), Texas (Stevenson and Griffith 1946, Allen 1952, Hunt and Slack 1989, Chavez-Ramirez 1996, Nelson et al. 1996, Westwood and Chavez-Ramirez 2005). Hunt and Slack (1989) reported that crabs constituted 42.9% and 40.1% of the total mean volume of winter food consumed by Whooping Cranes during the winters of 1983–1984 and 1984–1985. Chavez-Ramirez (1996) found that crabs made up a mean of 90.2% (62–98%) and 61.5% (18.4–97.6%) of their daily energy uptake during the winters of 1992–1993 and 1993–1994. A single study (Greer 2010) does not consider crabs to be a significant component of winter diets of Whooping Cranes. We hypothesized a causal linkage between crab abundance and mortality of Whooping Cranes for the following reasons: (a) cranes established large feeding territories in order to sequester food resources for themselves and their offspring (Crook 1965); (b) territories were located in areas where crabs were abundant and could be taken readily by cranes; (c) crab utilization by cranes was highly variable suggesting that there were periods when crab abundance could be critically low.

METHODS

Field Methods.—Pugesek et al. (2008) demonstrated that sampling crabs during the latter part of March provided a reliable and consistent measure of inter-year variability in crab abundance at Aransas NWR. Our methods controlled for factors that influence crab availability to cranes, including water levels and clarity, salinity, seasonality, crab reproductive patterns, and habitat variability. Data collection on crab abundance in March (Mar 15–30) was conducted in 1998–2006 in the coastal salt marsh along the eastern edge of Blackjack Peninsula of the Aransas NWR located on the southeast coast of Texas. The marsh lies parallel to the Intracoastal Waterway and is bordered by Dunham and Sundown Bays. We established two transects consisting of 12–14 100-m sections in two areas of the marsh (transects A and B; see Pugesek et al. 2008). While walking through the marsh over 3 days, we counted crabs and then calculated averages per 100-m section.

Whooping Cranes were censused via aerial survey weekly from mid-October through April. Flights of approximately 7-hr duration were conducted in a Cessna 172 (high-wing aircraft) with a contract pilot and one observer. Transects approximately 400 m apart were flown at 70 m altitude at 80 knots over the entire winter range of wild Whooping Cranes. The track of the aircraft was monitored on a hand-held GPS unit to ensure that no areas were missed. We divided the winter range into small blocks that received complete coverage before we moved on to the next area to minimize the chance of a duplicate count from local movements of cranes. All cranes sighted were plotted on aerial photographs. Approximately 95% of all cranes were located during a single census flight.

Adult cranes form pairs and almost always return to the same territories each winter, with pairs aggressively excluding other Whooping Cranes from their territory. From the weekly census flights, we delineated territories where a pair of birds was found every week without other cranes close by. Adult pairs stayed together throughout the year. Juvenile Whooping Cranes stay with their parents for their first year, with separation occurring occasionally late in the spring at Aransas or in the spring migration. Juveniles that separate from their parents at Aransas remain in the vicinity and continue to be sighted on census flights. Mortality was detected when one territorial adult or its juvenile disappeared. In the winter of 2001–2002, for example, 136 territorial adults and 15 juveniles were present, accounting for 151 out of the total flock size of 176. Thus, mortality could be readily detected on approximately 86% of the flock, and this value remained consistent from year to year; mortality goes undetected on the remainder of the population unless in rare instances a carcass is recovered or a sick bird that is practically immobile disappears. Sub-adult cranes wander between territories and will stray on rare occasions from the usual wintering grounds (Stehn 1992b). Also, based on one observation, an adult crane may lose its mate and re-pair within 72 hrs (Stehn 1992a). The exceptional case of rapid re-pairing may also cause mortality to be underestimated.

Statistical Analyses.—We used a non-linear regression analysis (Proc NLIN; SAS Institute 2003) to examine yearly measures of juvenile and adult mortality in relation to crab abundance. Mortality data were fit to the equation: $Y = 0.1\beta_{0-e^{-\beta 1 * X}}$, where Y was juvenile or adult mortality, β regression coefficients, e the exponential function, and X was the number crabs per 100-m section.

RESULTS

Crabs per 100 m of marsh varied widely from year to year, ranging from a low of 0.1 crabs per 100 m in 2001 to 3.4 crabs per 100 m in 2003 and 2004. Juvenile mortality was highest in 2001 and 2006 (2 and 4 juveniles) when crab counts were lowest (Table 1). The non-linear regression model was significant ($F_{2,7} = 7.22$, $P = 0.020$).

Adult mortality was high in 2001 (4 adults), which also corresponded to the year of lowest crab abundance (0.1; Table 1). Adult mortality was 1 per year during years of intermediate values of crabs (0.2–1.6) per 100 m (1998, 2000, 2002, 2005 and 2006) and 0 during years where high numbers of crabs (≥2.4) were counted (1999, 2003, 2004). Fit of the non-linear regression model to adult mortality was significant ($F_{2,7} = 24.30$, $P < 0.001$).

TABLE 1. Crab counts and juvenile and adult mortality of Whooping Cranes in 1998–2006.

Year	Crabs per 100 m	Juvenile mortality	Adult mortality
1998	0.4	0	1
1999	2.4	0	0
2000	0.6	0	1
2001	0.1	2	4
2002	0.8	1	1
2003	3.4	1	0
2004	3.4	1	0
2005	1.6	1	1
2006	0.2	4	1

DISCUSSION

Greer (2010) studied foraging behavior of Whooping Cranes and concluded that blue crabs were of lesser importance to cranes as a food source than previously described (Hunt and Slack 1989, Chavez-Ramirez 1996). She described cranes as generalists that followed a pattern of optimal resource utilization in which crabs were not particularly important. Similar to our findings, in season one of Greer's (2010) study from 2004–2005, crabs were more abundant than in season two, 2005–2006, and were utilized more heavily than in season two. Also similar to our findings (Pugesek et al. 2008) was Greer's (2010) determination that crab size was positively correlated to crab abundance. Thus, the combined effect of crab abundance and size further accentuates the disparity in food supply for cranes between years of high and low crab abundance. However, it appears that the years for Greer's (2010) study occurred when crabs were not especially abundant. Thirty seven percent of the juvenile and adult mortality that we observed in our study (7 of 19 mortalities) occurred in those two years. In year one of her study, measured crab abundance was less than half that of the maximum that we observed in nine years, while in year two it was the second lowest of the nine years of our study. During the second year of Greer's (2010) study we recorded 5 combined juvenile and adult mortalities, the second highest in our study, surpassed only by 6 mortalities in 2001, the year of lowest crab abundance in our study. The high mortality that we observed in those years supports the conclusion that blue crabs are critical in the diet and the survival of Whooping Cranes.

Our results further underscore the importance of longitudinal data collection (Pugesek and Wood 1992). Taken together, the results of Hunt and Slack (1989), Chavez-Ramirez (1996), Greer (2010), and our data suggest that crab abundance is highly variable and critical to the survival of the over-wintering Whooping Cranes. This relationship is non-linear where mortality is high during years of low crab abundance and declines towards zero during years of high abundance. Therefore, we believe it is important that levels of crab abundance remain above 0.4 per 100 m to insure high adult and juvenile crane survival. Freshwater inflows are a key element in maintaining a large and viable blue crab population (Longley 1994).

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Notes on the nesting behavior of the Half-collared Gnatwren (*Microbates cinereiventris*) in southeastern Peru

Jaime A. Garizábal[1,4] and Gustavo A. Londoño[2,3]

ABSTRACT.—*Microbates cinereiventris* is a polytypic and widely distributed species. Its reproductive behavior is only known based on the description of a single nest. Here, we present the first description of the eggs and nest of the subspecies *M. cinereiventris peruvianus* and the first description of the nestlings, feeding, and incubation behavior for the species. *M. cinereiventris peruvianus* has an open nest, primarily made of dry plant fibers and green moss. Nest attentiveness was 92.31 ± 0.20%, and a total of eight trips were recorded during the last 2 days of incubation. Nestlings hatched naked, were fed 1.58 ± 0.89 times per hour by both parents, and grew at a rate of 0.83 g per day during the first 5 days. *M. cinereiventris* share nesting characteristics with closely related species (*M. collaris* and *Ramphocaenus melanurus*). *Received 26 September 2012. Accepted 20 March 2013.*

Key words: Half-Collared Gnatwren, *Microbates cinereiventris*, nesting behavior, southeastern Peru.

Microbates cinereiventris is a widely distributed species in the Neotropics from Costa Rica to southeastern Peru and western Bolivia, mostly below 750 m (Hilty and Brown 1986, Atwood and Lerman 2006). In the southernmost part of its range, *M. cinereiventris* has a patchy distribution and is considered uncommon by Schulenberg et al. (2007). This species inhabits the understory of primary and secondary forests, and occasionally the forest edge, feeding mainly on ants and other small insects and spiders (Hilty and Brown 1986, Atwood and Lerman 2006, Schulenberg et al. 2007).

A poorly known Neotropical genus, *Microbates* is composed of two allopatric and polytypic species (Olson 1980, Atwood and Lerman 2006). This genus and *Rhamphocaenus* form a group with unclear relationships within the passerines (Rand and Traylor 1953, Kiff 1977). They have been considered within several families including Syilviidae (Rand and Traylor 1953), Troglodytidae (Sibley and Ahlquist 1991, Johansson et al. 2008), and Polioptilidae (Remsen et al. 2013). General aspects of their natural history are poorly known (Atwood and Lerman 2006). Although the nest and eggs of the Half–collared

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FIG. 1. Nest location (A) and nest architecture (B–D) of *Microbates cinereiventris peruvianus*.

Gnatwren (*Microbates cinereiventris*) have been described based on one nest found in Costa Rica (Kiff 1977), nothing is known about nesting behavior and nestling development. Our main objective is to provide the first description of the nesting behavior of *M. cinereiventris* and nestling development, and in particular incubation and feeding behavior.

METHODS

Our observations and descriptions are based on a single nest of *M. cinereiventris peruvianus* (*sensu* Olson 1980) found in a lowland forest with canopy height of approximately 35 m. This forest was located at the Pantiacolla Lodge, adjacent to the Alto Madre de Dios River, in the department of Madre de Dios, southeastern Peru (12°39′26.9″S, 71°15′05.7″W; 449 m). To document incubation behavior, we used two thermocouples attached to a HOBO–U12 data logger device with an accuracy of ±0.36 °C (Onset Computer Corporation, Bourne, Massachusetts, USA), which was set to record temperatures every minute. One of the thermocouples was placed under the eggs to record nest temperature, and the second thermocouple was placed 20 cm from the nest to record ambient temperature. We analyzed incubation behavior following Cooper and Mills (2005), using data from 32 consecutive hours during the last 2 days of the incubation stage. After hatching, we installed a Reconyx PC–85 camera (Rapid Fire Professional Color IR) for 3 consecutive days (80 hrs). The camera was set to take one picture every minute and eight consecutive pictures every time movement occurred between the camera and the nest (0.5 m apart). Nest, eggs, and nestlings were measured to the nearest 0.01 mm with a caliper and weighed to the nearest 0.05 g with a digital pocket scale. Mean values are presented as means ± SD.

OBSERVATIONS

Nest and Location.—On 12 November 2010, we found a nest of *M. cinereiventris* in a *terra firme* forest in a relatively open understory area. It was placed within the leaves of a palm (*Geonoma* sp.) at 0.45 m above ground (Fig. 1A). The nest was a bulky open cup with inner diameter of 51.7 × 51.5 mm and 45.2 mm in depth, outer diameter of 83.3 × 108.2 mm and a height of 56.7 mm. Additionally, the nest had hanging moss at the bottom that was 65.8 mm in length. The nest mass

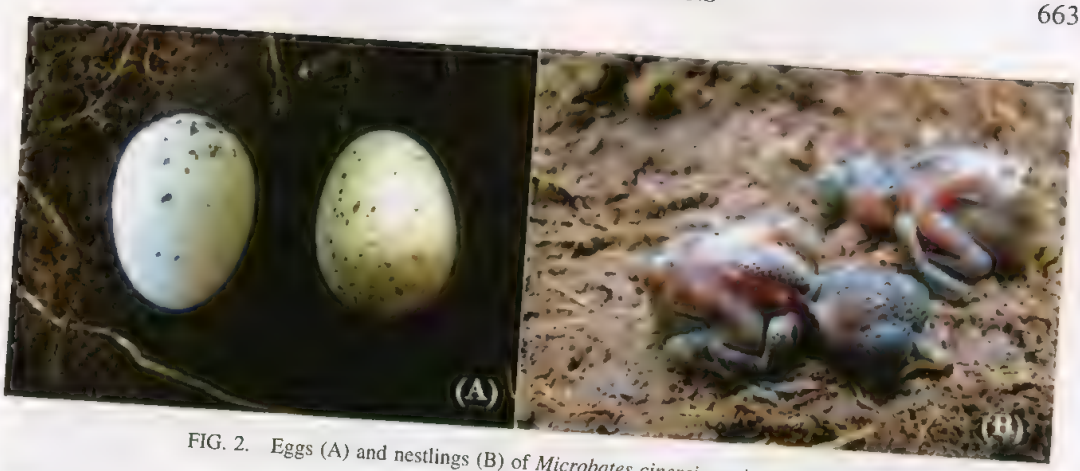

FIG. 2. Eggs (A) and nestlings (B) of *Microbates cinereiventris peruvianus*.

was 16.8 g and it was composed of three layers (Fig. 1). The outer layer (9.2 g) was composed of abundant green moss (4.8 g), palm dry leaves (0.4 g), and other plant materials (e.g., 4.0 g; sticks, rachises, and fibers) (Fig. 1B). The middle layer (4.9 g) was composed of dry angiosperm leaves (0.4 g), green moss (0.8 g), dry palm leaves (0.5 g), and other plant materials (3.2 g) (Fig. 1C). The inner layer (1.9 g) was composed of two types of fine plant fibers (0.1 and 1.8 g, respectively) (Fig. 1D).

Eggs and Nestlings.—The nest at the time of discovery contained two eggs with well-developed embryos. The eggs were white with a few reddish–brown and dark brown spots mainly at the broader end (Fig. 2A). They measured 19.1 × 13.8 mm and 18.3 × 13.8 mm and weighed 1.74 g and 1.64 g, respectively. The eggs hatched late in the afternoon of 16 November, according to thermal data on the nest. The following morning, the nestlings weighed 1.6 and 1.5 g, their wings measured 5.5 and 5.0 mm in length, and their tarsi were 7.5 and 7.0 mm in length, respectively. The nestlings were completely naked with dark brown skin and their eyes were closed, their gapes were light yellow and pinfeathers were just beginning to be visible in all tracts except on the head (Fig. 2B). On 20 November (fourth day after hatching), the nestlings started to open their eyes, and head pinfeathers started to appear; the primary pinfeathers measured 3 mm, having already broken through the skin but without breaking sheaths. The nestlings grew at a rate of 0.83 and 0.82 g per day, with wings growing at a rate of 1.83 and 1.60 mm, and tarsi growing at a rate of 1.67 and 1.30 mm respectively, until 21 November (fifth day after hatching) when they were depredated by an unknown predator (the batteries in the camera failed and no photograph was taken).

Two days prior to egg hatching, nest attentiveness was 92.31 ± 0.20% and the incubating parent(s) conducted four trips per day. On average, the parents spent 110.43 ± 93.71 mins incubating (min-max = 5–30 mins) and 8.62 ± 11.14 mins foraging (min-max = 1–35 mins). The night bout lasted 1,008 mins starting at 1257 hrs on the first day and finishing at 0546 hrs on the second day. Nest temperature was 29.97 ± 1.79 (min-max = 24.24–35.96 °C) and ambient nest microclimate was 24.90 ± 2.36 (min-max = 21.29–30.82 °C). The parent(s) spent all night brooding during our nestling observations (710 ± 24.58; min-max = 695–739 mins). Nestlings were fed by both parents 20.1 ± 13.1 (min-max = 5–30 trips/day) at a feeding rate of 1.58 ± 0.89 trips/hr, with larvae or worms (17.31%; 0.5–1.5× bill size), insects (9.61%; 1.5× bill size), and unidentified items (73.08%; <0.5× bill size). We observed seven feeding events while an adult was brooding. In 42.8% of the occasions, the brooding parent ate the item, and in the other 57.2% the brooding parent delivered the food to the nestlings. We recorded fecal sac consumption on five occasions and only one removal event.

DISCUSSION

We describe, for the first time, the nestlings, incubation, and feeding behavior of *Microbates cinereiventris*, and the nest of *M. c. peruvianus*. Our nest was similar to the one described by Kiff (1977) for *M. c. semitorquatus*. The clutch size, eggs, nestlings, nest, and nest site of *M. cinereiventris* are similar to *M. collaris* (Oniki

and Willis 1979) and *Ramphocaenus melanurus* (Eisenmann 1953, Skutch 1960). Gnatwrens attached their nests at broadleaf palms or shrubs in the understory less than 1 m off ground. They lay two white eggs with a few reddish–brown and dark brown spots, and their nestlings have yellow or orange–yellow gapes and are completely devoid of natal down at birth (Skutch 1960, Oniki and Willis 1979). However, as suggested by Kiff (1977), materials in the outer walls of the nest in *M. cinereiventris* could differ from other Gnatwrens. In Costa Rica, Skutch (1960) found a nest of *R. melanurus* with an outer layer of green moss in a path of Selaginella, unlike the nest described by Eisenmann (1953) of the same species in Panama, which had an outer layer of dry hanging leaves. Similarly, the only nest of *M. collaris* (Oniki and Willis 1979:101) to be described was said to be "a well concealed nest [that] looked like a pile of debris" without any green moss like *M. cinereiventris*. This variation of nest material used in the outermost layer has also been reported in the gnatcatchers (*Polioptila* spp.), which use different lichens in the outer layer of their nests depending on the habitat, even when comparing conspecific pairs (Chamberlin 1901).

As other members of Polioptilidae (*sensu* Remsen et al. 2013), both sexes of *M. cinereiventris* share activities while nesting, including nest construction (Kiff 1977), caring for the nestlings, and probably incubation. Our observed feeding rate (1.58 times/hr) was much lower compared to *Polioptila plumbea* (12.3 times/hr; Skutch 1960) and *R. melanurus* (4.5 times/hr; Skutch 1960). Our low feeding rates could result from only having observations during the early stage of the nestling period. Alternatively, altricial nestlings that lack substantial feather growth probably require less food and more brooding than they do later as they develop (e.g., O'Conner 1984, Rosa and Murphy 1994, Sockman 1998).

Nesting behavioral data support a close relationship between *Microbates* and *Ramphocaenus*, but as noted by other authors (Kiff 1977, Oniki and Willis 1979), these data failed to clarify the relative position of the Gnatwrens within the oscines. There are some traits of nesting biology like eggs, nestlings, and incubation rhythm, that suggest a close relation between *Microbates–Ramphocaenus* and *Polioptila* spp. Nevertheless, there are some remarkable similarities of nesting biology between *Microbates, Ramphocaenus* and some Old World genera of Sylviidae (*sensu lato*) (see Skutch 1960) and some shared differences with Troglodytidae, especially in nest architecture, that make it difficult to identify patterns and understand behavioral discrepancies. These birds could be reflecting ecological convergence and niche partitioning, both processes difficult to confirm and interpret without any integrative approach involving detailed data and analysis.

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Notes on Reproductive Biology of Two Species of Cracids in Northeastern Brazil

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ABSTRACT.—We describe nests, eggs, and some breeding aspects of the Rusty-margined Guan (*Penelope superciliaris*) and Speckled Chachalaca (*Ortalis guttata*) in the Atlantic Rainforest of northeastern Brazil. Two active nests of *P. superciliaris* were found, the first was 50 cm above the ground and the second was 2.6 m. Both were bowl shaped and had three and two eggs, respectively. One egg from each nest was measured and weighed: 64.3 × 42.1 mm (61.5 g) and 55.5 × 38.0 mm (42.5 g). An active nest of *O. guttata* was found 3.2 m high on top of a tree. Initially, there was a single egg in the nest but two more were laid. The average egg measurements and weight were 55.0 × 38.4 mm and 43.3 g. The eggs of both species were rather similar with a dull white color, rough shell, and smeared with organic matter from the nest. We observed an incubation period of 29–30 days for the chachalaca, which was longer than previous estimates of this species. The guan nests were found in an advanced stage of development, which prevented accurate tracking of their incubation periods. Although the primary social reproductive strategy in most cracids is monogamy, it is possible that *P. superciliaris* is polygynous in our study area, justifying the absence of a male near the nest or even a nest territory.

Key words: breeding, Cracidae, life history, Rusty-margined Guan, Speckled Chachalaca.

Cracids are gallinaceous birds found in Neotropical regions and include three distinct groups: chachalacas, guans, and curassows. They are predominantly arboreal inhabitants of forest, woodland, and scrub, and feed primarily on plant parts, thus playing an important role in dispersion of certain plant species (del Hoyo 1994, Brooks and Fuller 2006). Habitat loss and persecution from hunters are the two major threats faced by cracids, making this family the most threatened in the New World, with approximately one-half of the species threatened with extinction (del Hoyo 1994, Brooks and Fuller 2006, Brooks and Strahl 2006).

The Speckled Chachalaca (*Ortalis guttata*) and Rusty-margined Guan (*Penelope superciliaris*) are regularly reported in the Atlantic Rainforest

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FIG. 1. Female Rusty-margined Guans incubating nests, Rio Grande do Norte, Brazil. (A) Nest near the ground among bromeliads leaves; and (B) another nest in the low canopy. Photographs by Guilherme S. Toledo-Lima.

of northeastern Brazil (Schulz-Neto 1995, Silveira et al. 2003, Telino-Júnior 2005, Farias et al. 2007). Data regarding their life histories and breeding aspects in Brazil, such as clutch size and incubation period (Euler 1900, Ihering 1900, Sick 1997), are scarce, perhaps because of their discreet behavior, local extinctions, or low densities experienced by some populations in unprotected areas (del Hoyo 1994, Pereira and Wajntal 1999, Brooks and Fuller 2006).

The study of tropical bird life history traits is important to address questions highlighting differences between temperate and tropical species (Martin 1996, Stutchbury and Morton 2001, Tarwater and Brawn 2010). Nevertheless for many species of tropical birds descriptions of their nests or eggs do not exist (Marini et al. 2010). Therefore, many field researchers have been involved increasingly in providing descriptions and detailed studies about bird breeding in the Neotropical realm (Vasconcelos et al. 2006, Londoño et al. 2007, Bodrati and Castillo 2008, Lima et al. 2010).

During our current fieldwork focusing on the demography and breeding biology of birds in northeast Brazilian Atlantic Rainforest, we encountered active nests and captured and marked young cracids for a monitoring program. This experience provided us with descriptions and measurements of the nests, eggs, and other aspects of reproduction of the Speckled Chachalaca and Rusty-margined Guan.

OBSERVATIONS

We reported nests and juvenile birds in the Barreira do Inferno Launch Center (05° 54′ S, 35° 10′ W), a protected military area that harbors ~1,800 ha of tropical semideciduous lowland forest, located in Parnamirim Municipality, Rio Grande do Norte, Brazil. The nests were revisited on alternate days to check contents and estimate incubation period. Nest classification follows Simon and Pacheco (2005) and egg shape follows Baicich and Harrison (1997). To reduce the risk of nest disturbance, we took many precautionary measures such as avoiding egg or chick handling. Birds were trapped in mist nets and marked with numbered aluminum leg bands supplied by CEMAVE/ICMBio.

Rusty-margined Guan.—On 2 February 2012, two active nests were found: one contained three and the other two short subelliptical, white and rough eggs with dark stains from the moist leaves and twigs which composed the internal chamber. One egg from each nest was measured and weighed: 64.3 × 42.1 and 55.5 × 38.0 mm and 61.5 and 42.5 g, respectively.

The first nest was discovered among terrestrial bromeliad leaves (*Aechmea aquilega*) 50 cm above the ground with three eggs in advanced development. Besides some dry bromeliad leaves that supported the entire nest, a shallow basket that shaped the internal chamber was composed of leaves of *Anacardium occidentale* and several twigs and leaves of plants from the Myrtaceae family, apparently gathered while green (Fig. 1). The nest had a low cup/base and its measurements were: largest external diameter = 45.0 cm, smallest external diameter = 35.5 cm, largest chamber diameter = 38.5 cm, smallest chamber

FIG. 2. (A) One of the young Speckled Chachalacas captured in Barreira do Inferno Launch Center, Parnamirim, RN, Brazil. (B) The non-hatched Speckled Chachalaca egg collected on 5 March 2012. Photographs by Tonny M. de Oliveira Junior.

diameter = 26.0 cm, external height = 19.0 cm, and depth = 8.0 cm. On 10 February 2012, the nest was found only with eggshells and no evidence of predation.

The second nest of *P. superciliaris* was 2.6 m above the ground and low cup/fork in structure, placed within interlaced branches of two paired trees (*A. occidentale* and *Myrcia* sp.). The nest contained two eggs in the incubation chamber, and another on the ground in the leaf litter under the nest; this egg was probably rejected or dropped during incubation and was collected. The nest was bowl shaped and was made with twigs and leaves recently removed from either the support plants or the same species in the vicinity (Fig. 1). On 10 February 2012, we flushed an adult from the ground below the nest, where there was a broken egg. Apparently the nest was depredated, and the damage prevented us from taking measurements.

On 20 August 2011, we captured an immature guan (mass = 514.5 g) which was probably born during the breeding season of the same year. The plumage and morphology were similar to an adult (mass = 950–1,150 g; del Hoyo 1994), but the bird was smaller with a duller supercilium than adult birds.

Speckled Chachalaca.—An active nest of *Ortalis guttata* was found on 3 February 2012, approximately 3.2 m high on top of a tree of *Myrcia* sp. among dense foliage also formed by a liana plant. The nest was low cup/fork with a basket and the internal chamber flat without any distinct material, and probably built with dry twigs and leaves of the support tree. Initially there was a single egg in the nest, but two more were laid: one the following day and the last probably on 5 February, but it was not observed until the morning of 6 February. The eggs had a short subelliptical shape, were dull white, and had a rough shell that was smeared with organic matter from the nest and possibly some female blood. The egg measurements were: 53.4 × 37.0, 55.4 × 38.4 and 56.3 × 39.7 mm and weighed 39.75, 43.25 and 46.75 g, respectively. We observed an adult bird that flushed from the vicinity of the nest on several occasions when the nest was inspected, while another bird (probably the female) remained motionless in the nest only leaving when several researchers approached. During the morning of 5 March, the breeding pair of chachalacas could not be seen within the vicinity of the nest, which contained one intact egg and the other two had apparently hatched since there were no predation signs such as blood or chick remains. These shells were still wet and dirty with some residue; thus, we concluded the chicks hatched earlier that same day with an incubation period of approximately 29–30 days, considering a synchronic incubation. On the same day the nest was damaged by heavy rains, preventing accurate measurements. The non-hatched egg was collected and artificially incubated for three days, but the chick did not hatch (Fig. 2).

On 8 May 2011, we caught three young chachalacas that were ≤1 month old. They

weighed 70, 76 and 94 g (mean = 80 g). Their feathers were growing; the plumage was a brown coloration, darker on the back and brighter on head, breast, and abdomen. The small one had more downy plumage, including a wide black line extending from the crown to the nape, wing and tail feathers not fully developed, and the outer pair of rectrices was chestnut in color in contrast to the other which had browner plumage (Fig. 2).

DISCUSSION

Our observations regarding reproductive timing were similar to previous studies in southern Brazil. Specimens of *O. guttata* were collected in reproductive condition in October and November (Belton 1994), and *P. superciliaris* most likely had its breeding season between October and March (Mikich 1996). When additional studies in South America countries are combined, the main nesting season emerges as September through March (Brooks et al. 1993, Begazo and Bodmer 1998, Almendras et al. 1999, Bodrati and Castillo 2008, Herrera et al. 2009).

The reports on clutch size and egg characteristics follow the previous available descriptions for these species (del Hoyo 1994, Begazo and Bodmer 1998, Almendras et al. 1999, Bodrati and Castillo 2008, Herrera et al. 2009). The incubation period that we observed for *O. guttata* was longer than previous estimates of this species (e.g., 21 days; Sick 1997) and other congeners (24 days; del Hoyo 1994).

Nests of cracids are built at variable heights in forest vegetation and in different support plants (del Hoyo 1994), as we found guan nests ranging from 0.5 m in a bromeliad to 2.6 m on top of a tree. Furthermore, nests were chiefly constructed of material from the supporting plant or possibly collected from surrounding areas as reported in other cracid species (del Hoyo 1994, Bodrati and Castillo 2008, Herrera et al. 2009).

The primary social reproductive strategy in most cracids is monogamy, with the breeding pair staying together during incubation and defending intruders from the nest territory (del Hoyo 1994). We concordantly encountered a pair of chachalacas near the nest on several occasions. In contrast, we did not observe any birds near the guan nests while monitoring them except for the incubating females. There is insufficient information about the reproductive strategy used by *Penelope* sp., but other guans such as the Horned Guan (*Oreophasis derbianus*) and Highland Guan (*Penelopina nigra*) are perhaps polygynous (del Hoyo 1994, González-García 1995). It is possible that *P. superciliaris* is also polygynous in our study area, justifying the absence of a male near the nest or even a nest territory. More detailed studies are needed to clarify these issues.

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First Description of the Nest of the Hooded Berryeater, *Carpornis cucullata*

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ABSTRACT.—I describe the nest of the Hooded Berryeater (*Carpornis cucullata*), an endemic of the Atlantic Forest of southeast Brazil. On the basis of observations of six nests, three main types of nest placement were identified: (1) nests supported by forks, (2) nest totally supported by a single horizontal branch, and (3) nests erected at the base of the dense mass of

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stems growing from bamboo nodes. All six nests were structurally similar, with several twigs forming a superficial web, which constituted the surface of the incubatory chamber. Below and around this web, there was a loose to dense layer of supporting thicker sticks. The six nests also had in common the presence of a flexible liana-like fern, which lined the nests' external margin in a variable degree. In some respects, the nest of the Hooded Berryeater is similar to the nest of the congeneric Black-headed Berryeater (*C. melanocephala*), though they differ conspicuously in that the latter is mostly composed of large, dry leaves in the lower layer. *Received 5 March 2013. Accepted 3 May 2013.*

Key words: Atlantic Forest, Brazil, *Carpornis cucullata*, Cotingidae, Hooded Berryeater, nest.

The genus *Carpornis* (Cotingidae) is endemic to a narrow band of the Atlantic forest running from Alagoas to Rio Grande do Sul, eastern Brazil. It includes two species, the Hooded Berryeater (*Carpornis cucullata*), a mainly montane cotinga ranging from Espírito Santo to Rio Grande do Sul, and the Black-headed Berryeater (*C. melanocephala*), a mainly lowland taxon distributed from Alagoas to Paraná (Snow 1982). Although only the latter has been so far included in molecular phylogenetic studies (Tello et al. 2009), the monophyly of the genus has not been questioned. Indeed, these two vocally and morphologically similar species have been regarded as closely related (Snow 1982).

Of the 25 genera presently included in the Cotingidae, description of the nest is unavailable for five of them (Snow 2004, Belmonte-Lopes et al. 2011). Even though the egg of the Hooded Berryeater is described and illustrated in the literature (von Ihering 1900, 1901 [plate XI, no. 1]), its nest is still undescribed (Snow 1982, 2004; Kirwan 2009); the nest of the Black-headed Berryeater has been recently described (Belmonte-Lopes et al. 2011). Here, I describe the nest of the Hooded Berryeater on the basis of six complete nests found in the state of Rio Grande do Sul, southern Brazil.

METHODS

Breeding activities and behavior of the Hooded Berryeater were studied at Cerro das Almas (31° 46′ S, 52° 35′ W; 100–260 m asl), Capão do Leão municipality, Rio Grande do Sul, Brazil, between October 1998–April 2000. Cerro das Almas is a low granitic ridge, whose southeast-facing slope is covered by a 500-ha forest block, where the Hooded Berryeater has its southernmost distributional limit (Maurício and Dias 1998, 2001). I studied this species by following singing males. A territorial male of this cotinga typically sings from perch to perch in the mid-stratum quite regularly, commonly staying several minutes to more than an hour in the same fruiting tree (GNM, pers. obs.). This behavior allows one to approach and locate a given territorial male on a regular basis. In this way I located five nests at Cerro das Almas and another at Centro de Pesquisas e Conservação da Natureza Pró-Mata (hereafter CPCN Pró-Mata; 29° 30′ S, 50° 10′ W, 900 m asl), São Francisco de Paula, northeastern Rio Grande do Sul. All nests contained a single egg or nestling. Nests were described following the standard protocol of Simon and Pacheco (2005). Measurements were taken with a caliper to the nearest 0.1 mm. Abandoned materials related to nesting events were collected and deposited at the ornithological collection of Museu de Ciências e Tecnologia of Pontifícia Universidade Católica do Rio Grande do Sul (MCP), Porto Alegre, Rio Grande do Sul, Brazil.

RESULTS

All six nests were similar in composition and general structure. Several 50–80 mm long twigs, 0.5–1.0 mm in diameter formed a thin web which constituted the superficial lining of the incubatory chamber (Fig. 1); below and around this web there was a loose to dense layer of thicker sticks (generally 3 mm or more in diameter), much deeper in the two bamboo nests (see below). The six nests also had flexible rhizomes of a liana-like fern (possibly of the genus *Microgramma*, family Polypodiaceae), which lined the nests' external border in a variable degree (from a few stems to a dense and broad net) and had some pendent stems measuring a few centimeters to 450 mm long.

Nest placement was variable. Three nests matched the low cup/fork type of Simon and Pacheco (2005), with two having been erected in horizontal forks, showing the same supporting design as the nest of the Black-headed Berryeater (Fig. 2 in Belmonte-Lopes et al. 2011); the other nest was erected at the base of inclined and forked stems. All three nests were supported laterally by stems about 10 mm in diameter and by one or more thinner twigs at the bottom of the nest structure. One of these nests had an external diameter of about 100 mm in the wider portion and 74 mm along its narrower axis; the very shallow incubation chamber had a diameter of about 70 mm and was no more than 10 mm deep.

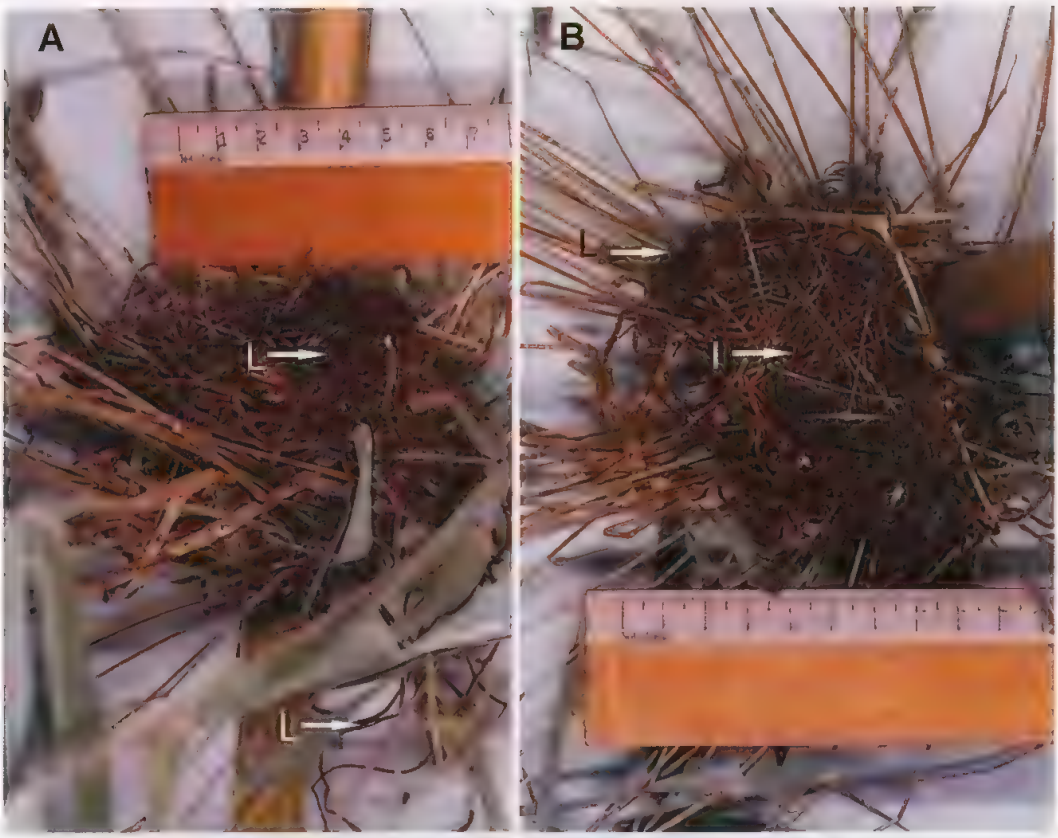

FIG. 1. Nest of the Hooded Berryeater, *Carpornis cucullata*, collected at Cerro das Almas, Capão do Leão, Rio Grande do Sul, Brasil (MCP 1151). A – Lateral view. B – View from above. Note the massive presence of a liana-like fern (L) lining the margin of the nest or pendent below it; also note the web of thin twigs forming the surface of the incubatory chamber (I). Scale in centimeters.

The other two nests of the same type were too damaged for adequate measurements but were similar in size and shape to the preceding one. All three nests were located in 6–10 m tall understory trees and were placed between 4.5 and 5.5 m above ground.

Another nest matched the low cup/base of Simon and Pacheco (2005), being totally supported by a single horizontal branch 100 mm in diameter of a 17 m tall *Cupania vernalis* tree. This nest had a diameter of 136 × 93 mm externally and of 68 mm internally, with the incubation chamber being 33 mm deep. The incubation chamber was placed toward the flank of the natural curvature of the circumference of the branch. Two thin branches emerging from the flank of the main branch served as secondary supporting points for the external wall. This nest was placed about 9 m above ground.

A third type of nest did not match precisely any of the standard types of Simon and Pacheco (2005), having some aspects in common with both the low cup/fork and the low cup/base types of these authors. This type corresponded to a nest built at the base of the dense mass of stems that usually grows from the bud of a bamboo node (Figs. 1, 2). Externally, this nest measured 84 × 95 mm and was 69.5 mm high. Its incubation chamber was 37–45 mm wide and 13 mm deep. The numerous stems that grew upwards from the bamboo node extended far beyond the nest border and formed a loose lateral wall for the nest. It was located 4.8 m above ground in a *Merosthachys* sp. bamboo which was part of a dense but small stand of 4–5 m^2. An additional nest was found and briefly studied at CPCN Pró-Mata. It was also placed among the dense clump of stems growing from a *Merosthachys* bamboo node, about 5 m

FIG. 2. General (lateral) view of the same nest shown in Fig. 1 (MCP 1151). Notice the numerous stems that grow upwards from the bamboo node, forming a loose lateral wall for the nest. Bamboo stem cut just above and below the nest.

above ground, and was similar in size and structure to the latter nest. It contained a 4–5-day-old nestling which was attended by the adults. A third nest, apparently of this same type, was found at a very early stage of construction at Monte Alverne, Santa Cruz do Sul (29° 34′ S, 52° 22′ W; 500 m asl.), on 28 October 1994 (A. Kindel and G. A. Bencke, pers. comm.). It consisted of a few twigs placed among the stems of a bamboo node, about 4 m above ground, also on a *Merostachys* bamboo.

All nesting sites were located inside primary forests with canopy between 15–20 m in height. Collectively, Cerro das Almas nests were active between October and March. The Pró-Mata nest was studied on 17–18 December 1999. The bamboo nest from Cerro das Almas was collected (MCP 1151) after the end of the breeding season.

DISCUSSION

The design and composition of the nest of Hooded Berryeater are consistent with its placement in the subfamily Cotinginae (*sensu* Ohlson et al. 2013), an assemblage of tropical forest species whose nests generally are small and flimsy structures composed of twigs and other woody materials (Snow 1982, 2004). In some respects, particularly in the presence of a web of thin twigs forming the lining of the incubatory chamber, the nest of the Hooded Berryeater is similar to the nest of the congeneric Black-headed Berryeater though they differ markedly in that the latter is mostly composed of large, dry leaves in the lower layer (Belmonte-Lopes et al. 2011). The nest of the latter species falls within the size range of the nest of the former. Nests of both species are inconspicuous. In the nest of the Hooded Berryeater, this attribute results from the addition of long and tangled rhizomes of a liana-like fern which produces the impression of an irregular mass of dark epiphytic plants that in no way resemble the typical shape of a nest (Figs. 1, 2), unlike the Black-headed Berryeater nest which resembles aerial leaf litter (Belmonte-Lopes et al. 2011).

The nests described here illustrate caution when making generalizations based on finding a single nest. When I encountered the nest placed on the bamboo node, which was the first to be found, I conjectured that the Hooded Berryeater might be specialized in bamboo nesting and that this would represent an anti-predatory adaptation benefited by the concealing effect provided by the long and massive stems that grow from bamboo nodes. Though nesting in bamboos may provide good concealment, most nests I found subsequently were all distinct in their placements. The analysis of the six nests suggests that the anti-predatory component might be conferred by the usage of rhizomes of epiphytic plants in nest structure.

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Occurrence of hybrids between *Momotus momota* and *Baryphthengus ruficapillus* (Momotidae) in central Brazil

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Deborah F. N. de Oliveira,[2] and Gabriella Cardoso[2]

ABSTRACT.—We describe a hybrid between the Amazonian Motmot (*Momotus momota*) and the Rufous-capped Motmot (*Baryphthengus ruficapillus*), collected in northern Goiás, Brazil. In some characters (e.g., shape of the tail and facial mask) the hybrid is similar to *B. ruficapillus*, in others (e.g., measures and amount of blue in the plumage) it is intermediate between the two parents, and in others (e.g., color of the underparts) it is unlike any of them. Photographs document the occurrence of hybrids in two additional localities in Goiás. Complexity of the genetic control of plumage color in birds may explain the hybrid's characters, and rarity of *B. ruficapillus* may be a factor leading to hybridization between these species. This is the first known case of intergeneric hybridization in the Coraciiformes. *Received 4 February 2013. Accepted 3 May 2013.*

Key words: *Baryphthengus ruficapillus*, distribution, hybridization, Momotidae, *Momotus momota*, sympatry.

Hybridization is a common and widespread phenomenon among birds (Grant and Grant 1992). One in 10 species of birds is known to have naturally hybridized with another species (Grant and Grant 1992). Thousands of crosses between bird species both in the wild and in captivity were described by McCarthy (2006).

Identification of hybrids may be a difficult task (Graves 1992), and explicit assumptions must be made concerning the expression of characters in hybrids (Graves 1990). We assume that hybrid characters can be expressed in three ways, as defined by McCarthy (2006): intermediacy, combination, and heterosis. In the first, the character presents an intermediate state between those of the parent species. Less commonly, the hybrid is similar to one parental species regarding some traits but similar to the other in different traits (combination). Finally, the hybrid can also be heterotic, that is, depart widely from the range of variation of both parental species in a given character.

The Amazonian Motmot (*Momotus momota*) is found in a wide variety of wooded habitats, from humid rainforest to semi-arid open woodland (Sick 1997, Snow 2001) in South America south and east of the Andes, including the entire Amazonian Basin, most of the Brazilian Cerrado, and reaching northern Argentina, with an isolated population in the Atlantic Forest of northeastern Brazil (Sick 1997, Snow 2001). The Rufous-capped Motmot (*Baryphthengus ruficapillus*) ranges mainly in the Atlantic Forest of southeastern Brazil, eastern Paraguay, and northeastern Argentina, extending into Goiás in central Brazil, where it is known to be sympatric with *M. momota*. It inhabits the interior of humid forest (Sick 1997, Snow 2001). We report a case of hybridization between *M. momota* and *B. ruficapillus*. This is the first known case of intergeneric hybridization in the Coraciiformes and the second known case of hybridization in the family Momotidae (McCarthy 2006).

METHODS

Study Area.—The hybrid specimen was collected in the municipality of Campinaçu, northern Goiás (13° 54′ 54″ S, 48° 30′ 13″ W). This area is located in the central part of the mainly savannic Cerrado biome. Our collections were made in *cerradão* woodland, the tallest of several phytophysiognomies found in the Cerrado (Eiten 1972, Cavarzere et al. 2011).

Material Examined and Analyses.—In addition to the hybrid, we collected typical individuals of *B. ruficapillus* and *M. momota* (see below), all within an area of about 2 km^2. We compared these specimens to series of *B. ruficapillus* (72 specimens) and *M. momota* (218 specimens) housed at the Museu de Zoologia da Universidade

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TABLE 1. Plumage characters that present differences between *Baryphthengus ruficapillus*, *Momotus momota pilcomajensis*, and their hybrid collected in Campinaçu. Capitalized color names and numbers follow Smithe (1975).

	B. ruficapillus	*M. momota pilcomajensis*	Hybrid
Forehead, crown, nape and hindneck	Uniformly Brick Red (132A)	Forehead Cerulean Blue (67), crown black, nape Smalt Blue (70) and hindneck Parrot Green (260)	Forehead and crown mixed Brick Red (132A) and Parrot Green (260), nape Cerulean Blue (67), hindneck Cinnamon (123A)
Sides of the head (except black mask)	Bunting Green (150)	Parrot Green (260)	Cinnamon (123A)
Black mask	Round or squared posterior end	Sharp posterior end	Squared posterior end
Blue along the margins of the black mask and chest spots	Absent	Present, conspicuous	Present, inconspicuous
Chin	Buff (124)	Bunting Green (150)	Cinnamon (123A)
Upper chest	Bunting Green (150)	Bunting Green (150)	Cinnamon (123A)
Lower chest	Antique Brown (37)	Raw Umber (123)	Cinnamon (123A)
Belly	Parrot Green (260)	Cinnamon (123A)	Intermediate
Tail rackets	Absent	Present	Absent
Undertail	Glaucous (79)	Blackish Neutral Gray (83)	Intermediate

de São Paulo (MZUSP), where we deposited the specimens collected in this study. In the following descriptions of specimens, capitalized color names and numbers refer to Smithe's (1975) color guide. We measured exposed culmen, bill width, bill height, tarsus, and wing and tail length of all specimens. In order to visualize the morphometric differentiation between the hybrid and its parental species, we conducted a Principal Component Analysis (PCA).

We reviewed photographs of birds identified as either species from the website WikiAves (www.wikiaves.com.br) in search of other possible hybrids. This is an extensive database on Brazilian birds and is generally considered trustworthy, but we nevertheless contacted authors of relevant photographs to confirm the circumstances under which they were taken.

Based on MZUSP specimens, WikiAves, and the literature (Hayes and Areco de Medina 1988, Hayes et al. 1990, Hayes 1995, Ericson and Amarilla 1997, Robbins et al. 1999, Esquivel and Peris 2008), we assembled a map of the records of *M. momota* and *B. ruficapillus* and their hybrids in south-central Brazil and adjacent Paraguay.

RESULTS

On 22 September 2012, while doing fieldwork in Campinaçu, LFS recorded a typical song of *M. momota*. Upon playback of this recording, an individual of typical appearance for this species approached and was collected (MZUSP 94584). Subsequently, LFS observed another pair, also attracted to the playback and perched nearby, side-by-side on the same branch. One member of the pair was collected (MZUSP 94582) and proved to be a hybrid between *M. momota* and *B. ruficapillus*, as described below. On the following days, three typical specimens of *B. ruficapillus* (MZUSP 94579, 94580 and 94581) and one more typical specimen of *M. momota* (MZUSP 94583) were collected. The last specimen was collected after being attracted to playback of the song of *B. ruficapillus*.

M. momota includes several subspecies (Snow 2001), but the birds collected in Campinaçu can be assigned to *M. m. pilcomajensis*, because of the greenish color of the upper chest and cinnamon color of the belly. All character comparisons were thus made in relation to this subspecies. *B ruficapillus* is monotypic and does not present significant geographical variation (Straube and Bornschein 1991).

The plumage characters of the hybrid and parental species are detailed in Table 1 and Fig. 1 illustrates the hybrid specimen in comparison with each parental type. Following McCarthy's (2006) classification of characters in hybrids, the colors of the belly and undertail, and the amount of blue in the mask and chest spots, are intermediate; the shapes of the facial mask and tail are as in *B. ruficapillus* (combination); and the colors of the chest and sides of the head are heterotic. The color pattern of the forehead, crown

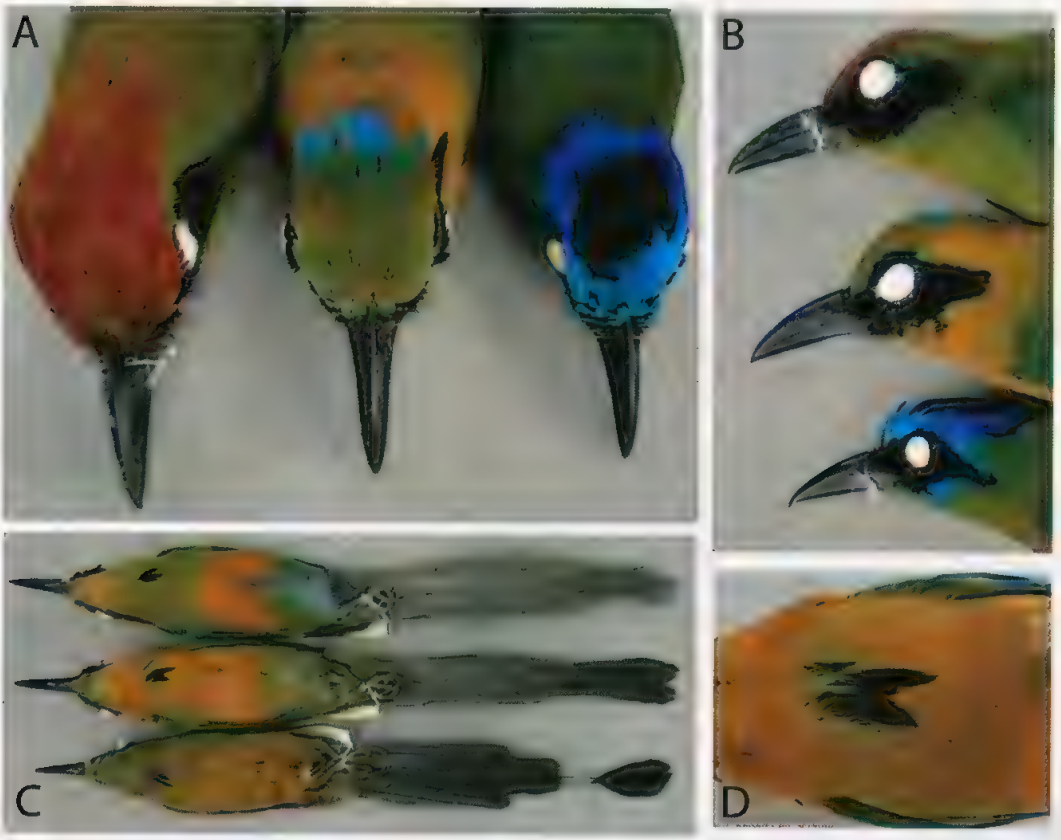

FIG. 1. Specimens of *Baryphthengus ruficapillus* (MZUSP 94580; left on A, top on B and C), *Momotus momota* (MZUSP 94584; right on A, bottom on B and C) and their hybrid (MZUSP 94582; D, and middle on A, B and C) collected in Campinaçu, Goiás. A: forehead, crown and nape. B: side of the head and facial mask. C: ventral view of the specimens. D: detail of the hybrid's pectoral spot showing blue feathers.

and nape is difficult to fit into any category. The Brick Red background resembles *B. ruficapillus*, but is mixed with green, which is not present in the head of either parent. The nape is Cerulean Blue, and while this color is present in the forehead of *M. momota*, this species' nape is mostly Smalt Blue. In the PCA (Eigenvalue: 97.54%), *B. ruficapillus* and *M. momota* formed two separate clusters, and the hybrid specimen appeared almost exactly between them, tending slightly more towards *M. momota* (Fig. 2).

Two more hybrids were identified in photographs found on WikiAves. The photographs were taken in the municipalities of Cocalzinho de Goiás (WA 437416) and Alexânia (WA 76880), in central Goiás (Fig. 3). The birds in the photographs can be identified as hybrids by the narrow blue edgings and squared or rounded end of the facial mask, and by the uniformly Cinnamon underparts. Additionally, blue feathers can be seen in the pectoral spots of the bird from Cocalzinho de Goiás.

Range maps show that *M. momota* and *B. ruficapillus* are sympatric in an extensive region that extends from northern Goiás, through São Paulo, to Paraguay (Fig. 4). Across this area, both specimens and photographs of *M. momota* are more numerous than those of *B. ruficapillus*. Our records of *B. ruficapillus* in Campinaçu, along with some others from that region and from nearby Chapada dos Veadeiros, represent the extreme northern limit of its range.

DISCUSSION

In order to identify a bird as a hybrid, the hypothesis that it represents a valid, new taxon or a developmental variant of a known species must be rejected (Graves 1990). It is highly unlikely that our specimen represents a valid taxon, given

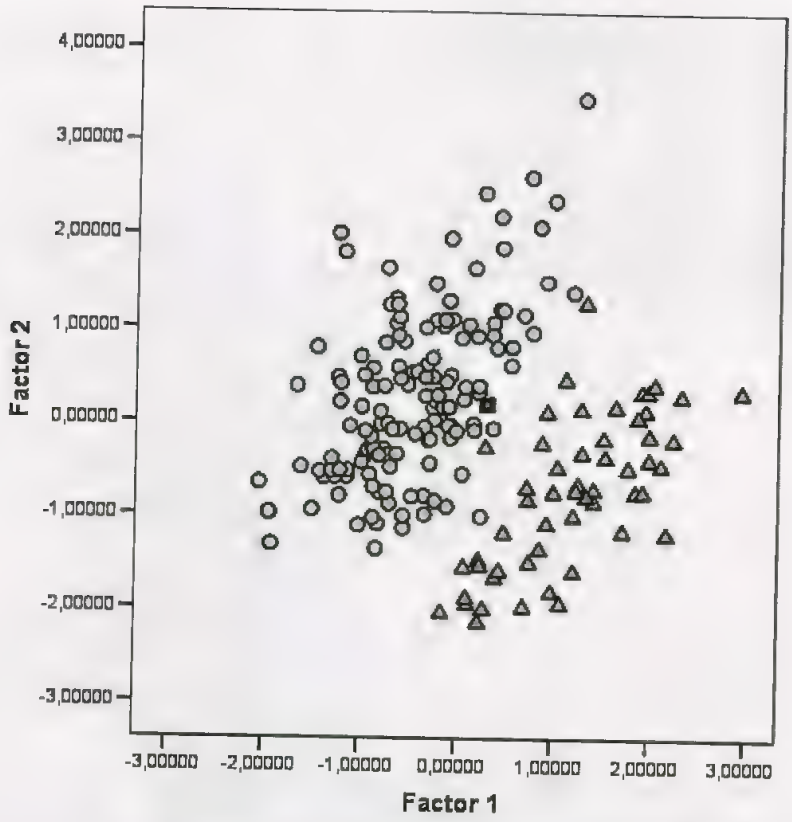

FIG. 2. Results of the Principal Component Analysis. The first factor explained 80.87% of the variation and was mostly influenced by tail length. Gray circles = *M. momota*; gray triangles = *B. ruficapillus*; black square = hybrid specimen.

FIG. 3. Photographs of hybrids published on WikiAves. Left, WA437416, taken by Roberto Aguiar in the municipality of Cocalzinho de Goiás; right, WA76880, taken by Bruno Salaroli in the municipality of Alexânia. The photographs have been cropped to show only the birds.

that (1) it presents characters of the only two species of motmot occurring in the area; (2) from a statistical standpoint, the possibility that a new taxon would be almost exactly intermediate in morphometrics between two species, as shown by the PCA, is very remote (Graves 1992); (3) it was paired with a typical *M. momota*; and (4) this pair was attracted to playback of the song of *M. momota*. The possibility that it is a juvenile of any species can also be discarded, given that its skull was fully ossified and that young motmots have essentially the same plumage as adults, only duller (Snow 2001). Thus, and considering that it expresses traits of *M. momota* and *B. ruficapillus* in the manner defined by McCarthy (2006) for hybrids, the hybrid hypothesis best explains the specimen's characters. *M. momota* and *B. ruficapillus*, the only motmots occurring in a radius of at least 1,000 km (the nearest other motmot being exclusively Amazonian *Electron platyrhynchum*), are the only possible parental species.

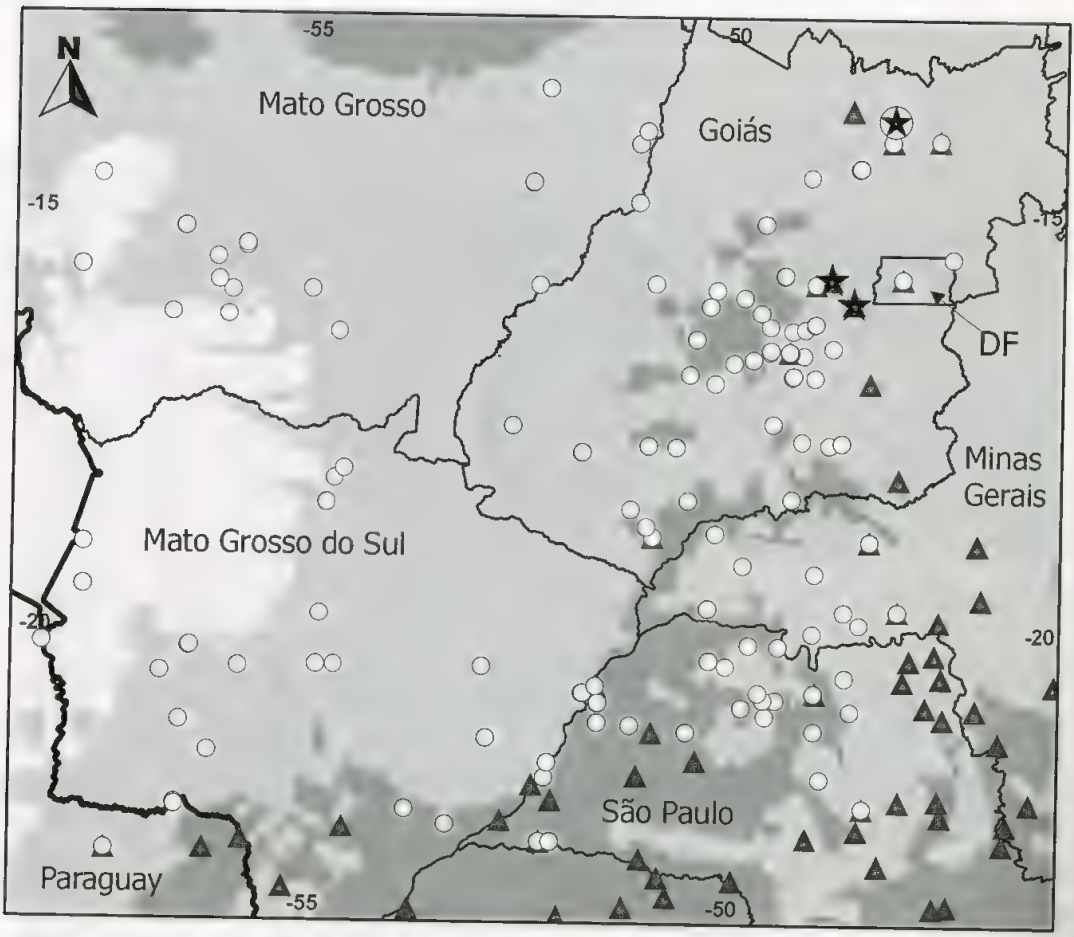

FIG. 4. Distribution of *Momotus momota*, *Baryphthengus ruficapillus*, and their hybrids in south-central Brazil and adjacent Paraguay. White circles = *M. momota*; gray triangles = *B. ruficapillus*; black stars = hybrids from the website WikiAves; black star inside a circle = hybrid specimen. Dark gray shading represents tropical and subtropical humid forests; pale gray shading represents grasslands, savannas, and shrubland. DF = Distrito Federal.

The complexity of character expression in the hybrid can be explained by the fact that genetic control of plumage color in birds appears to be separate for each class of pigment and for structural colors, and independent between feather tracts (Graves 1990). The complex pattern of coloration on the hybrid's forehead, crown, and nape may arise from interaction between the melanin-based pigments that are probably responsible for *B. ruficapillus*' rufous coloration and the structural blues of *M. momota*. The hybrid's Cinnamon-colored sides of the head and upper chest are harder to explain, as both parents are green in these regions. A possibility to explain these heterotic characters is atavism, that is, appearance in the hybrid of a character not present in either parent, but postulated to be ancestral in the group (Graves 1990). This hypothesis is supported by the fact that several closely related taxa, such as *Baryphthengus martii*, *Momotus subrufescens*, and *M. bahamensis* show a similar coloration in that plumage part (Snow 2001).

Based on a single specimen and two photographs, it is difficult to speculate on the possible causes of hybridization. It is significant, however, that the hybrids were found near the edge of *B. ruficapillus*' distribution and in regions where it is rarer than *M. momota*. A classic hypothesis to explain hybridization states that it may occur when one of the parental species is rarer than the other (Hubbs 1955, Grant and Grant 1992, Randler 2002). In such situation, scarcity of mate

availability may lead a female of the rare species to copulate with a heterospecific male. Thus, rarity of *B. ruficapillus* in relation to *M. momota* in central Brazil may be a factor leading to hybridization between these species.

ACKNOWLEDGMENTS

We thank Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for a grant (Evolução da Fauna de Vertebrados Terrestres Brasileiros do Cretáceo ao Presente: Paleontologia e Filogenia, CNPq 565046/2010-1) and a fellowship to LFS, and Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA – SISBIO) for collecting permits. We thank M. A. Rego, G. Del-Rio, G. Garbino, V. Cavarzere, M. Curry and an anonymous reviewer for discussions or commentaries on earlier versions of the text. B. Salaroli and R. Aguiar photographed the hybrid birds found on WikiAves.

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The Wilson Journal of Ornithology 125(3):680–683, 2013

Ornithological Literature

Margaret A. Voss, Book Review Editor

RUTA BARRANCOLI: A BIRD-FINDING GUIDE TO THE DOMINICAN REPUBLIC. By Steven C. Latta and Kate J. Wallace. Illustrations by Dana Gardner. Photographs by Dax Román E. National Aviary, Pittsburgh, PA, USA. 2012. 241 pages. ISBN: 978-0-615-62568-3. $29.95 (cloth).—This new bird-watching guide is a creative, well-conceived manual that will be much appreciated by anyone venturing to the Dominican Republic, researchers and travelers alike. The book displays an intimate knowledge of the avifauna found in this Caribbean country and provides a clear, efficient approach for the birdwatcher. *Ruta Barrancoli* is a model of organization, clarity, and functionality, and comes complete with 32 outstanding original plates by Dana Gardner showing each of the endemic species—reason enough for anyone interested in the birds of the region to own this guide. Further, the authors are regional bird experts. Dr. Steven Latta is the lead author of *Birds of the Dominican Republic and Haiti* and many scientific manuscripts describing avian ecology on the island, and Kate Wallace is the owner of Tody Tours, a guide service that evolved from her time as a Peace Corps volunteer in the country's rural Cordillera Central.

The guide begins with several interesting and concise introductory sections on 1) biodiversity and conservation; 2) geography and habitat; and 3) resources for the traveler. These are followed by one of the exceptional features of the book: a checklist and mini-field guide illustrated with original plates of the 32 endemic species. Mr. Gardner's plates show a smooth, calm artistry that delivers precise field marks and accurate postures and proportions. He has a tremendous ability to capture the essence of a species' appearance without getting bogged down in painting every feather. Each of his illustrations is a pleasure to view. These are followed by two useful tables: one that lists the 32 endemics and exactly where they are likely to occur, and another that lists the full avifauna of the country. Both are referenced to a clean, clear map situated immediately after the Table of Contents.

Then begins the real heart of the book. The authors divide the country into five sensibly bordered regions, based primarily on landscape characteristics, and devote the remainder of the book to describing each in detail. Each region is introduced with a map and a listing of the specific sites in the format of a "birding trail," as referenced in the book's title: *Ruta*, meaning path or route, and *Barrancoli*, which is the local name for Broad-billed Tody (*Todus subulatus*), a colorful endemic species. The authors then provide a unique species checklist for each region that is referenced to the region's sites and detailed with "targeted" and "probable" occurrences for each species. Following each checklist are detailed site descriptions (44 in total) that begin with a pop-out text box describing elevation, trail difficulty, hours of entrance, entrance fees, and geographic coordinates. Within the text are easy-to-follow sections providing site descriptions, access, addresses, websites, logistics, and detailed descriptions of kilometer-by-kilometer birding highlights. There are also nicely drawn mini-maps for each site which will help the birder remain oriented and sub-checklists that describe "target species" for each site. When the "going gets rough" in some of the more out-of-the-way sites, the authors do an excellent job of providing a high level of detail and many well-seasoned tips that will help travelers stay on track. One could effectively design a birding vacation or research expedition around the "birding trail" format of the book, or simply pick and choose among sites to reconnoiter with the birds of choice. The book ends with a definitive checklist of the birds of the Dominican Republic and provides their common names in English and Spanish, and a description of their conservation status.

Ruta Barrancoli provides a wealth of hard-won logistical information that would take the average traveler to the Dominican Republic many visits to begin to sort out. Most tourists in the Dominican Republic never leave the confines of resorts and therefore miss out on the bulk of the avifauna, not to mention the culture. The routes described in this book, in addition to providing some outstanding birding, would provide any visitor to the country with a rich cultural experience. Anyone inspired to do avian research in the Dominican Republic or to chase its 32 endemic bird species will find this book to be an essential tool on their adventure.—JASON

M. TOWNSEND, University of California-Davis, Department of Wildlife, Fish and Conservation Biology, Davis, CA 95616, phone: 530-750-9061, email: jmtownsend@ucdavis.edu

PETRELS, ALBATROSSES & STORM-PETRELS OF NORTH AMERICA: A PHOTOGRAPHIC GUIDE. By Steve N. G. Howell. Princeton University Press, Princeton, New Jersey, USA. 483 pp., several hundred color photographs, 3 color plates. ISBN: 978-0-69114211-1. $45.00 USD (hardcover).—After I began the second, at-sea phase of my research life, my love switched from alcids to the true birds of the deep ocean—the tubenoses. In preparation for this work, I assembled all of the few field guides I could locate for help in the field back there in the Dark Ages of the early 1980s: Alexander's (1928) *Birds of the Ocean* (believe it or not—but it gives you an idea of how little was available to us back then) and Harper and Kinsky's (1974) *New Zealand albatrosses and petrels: an identification guide*. Most importantly, I was extremely fortunate that Tuck's (1978) *A field guide to seabirds of Britain and the world*, a quantum improvement over everything published prior to that, came out not long before I headed to Japan in 1982 for my first research cruise in the deep North Pacific. That book helped me begin to understand the main field marks and to begin learning about at-sea distribution in this poorly known region. Then, in 1983, Peter Harrison's incredible *Seabirds: an identification guide* came out. It was another quantum leap for seabird researchers who were surveying large areas for which little distributional information was known, so we had to be on our toes for just about anything. Peter also had seen a vast majority of the birds in his book, which really gave him a leg up on describing them. Although his plates clearly show an affinity for *Pterodroma* petrels but not *Puffinus* shearwaters, which in my opinion are poorly done, the book was invaluable overall, and I wore my first copy out in a few years. He soon followed this *tour de force* with his 1987 book *Seabirds of the world a photographic guide*.

Oh, that I had had a copy of Steve Howell's *Petrels, albatrosses & storm-petrels of North America: a photographic guide* with me when I was first starting out! This is one of those books that you read and realize that this is an opus. Just about every page has a few jewels of information that could be gleaned only by spending enormous amounts of time at sea looking at tubenoses—and remembering it all.

The book is organized with the usual introductory material: what are tubenoses, marine habitats (the ocean may look all the same flat and wet, but it isn't), phylogeny (there are a lot of ways to skin this cat), broad-scale taxonomy (i.e., characteristics of families), main points about field identification of the main groups (including molts, plumages, and aging), and threats and conservation (as a group, these are some of the most at-risk species of seabirds in the world). This introductory material takes up more than 10% of the entire length of the book, but it is worth it because there you realize that this is an authoritative book. In particular, the section on molts, plumages, and aging walks you through some very difficult material in such a way that you actually understand it at the end.

The meat of the book, however, is the detailed species-accounts for about 70 species that have been recorded on either coast of North America. For each species, there is a summary of the overall size of the bird, main points of identification, taxonomy, meaning of the scientific and common names, status and distribution (Pacific and Atlantic are dealt with separately, and there are quite good range maps—although maps are not shown for all species that are rare in North America), similar species, habitat and behavior, identification (including both the air and water), and molt. Each account is accompanied by a few to many photographs taken of the species in a variety of situations, light conditions, and locations (on the wing, on the water); in fact, it is the first place I have seen a photograph of the Bermuda Petrel (Cahow) in flight, rather than in somebody's hands. Each photo has a caption where Howell brings his extensive experience to describe how/why this photo represents this bird under these specific observation conditions and it could not be another closely related species. It really is an astounding set of photographs and an astounding breadth of information in the captions.

As fantastic as this book is, I do have two main problems with it. These problems involve primarily the taxonomic approach and the at-sea distributional maps. Howell's taxonomy follows some of the recent genetic studies, although why he picked some and not others to follow is unclear. However, he is clear (p. 16) that the taxonomy of this group is still in flux, so this is not touted as the final say on taxonomy. For example, those who use this book have to deal with the small shearwaters still being called *Puffinus* but the large ones now being called

Ardenna; for those of us who learned them so long ago and think of them as just ecological variations on a theme, these changes can be a bit jarring, especially when we realize that the taxonomy is not settled. Another aspect of the taxonomy that is a bit unusual is that he approaches most or every identifiable form as a separate species—presumably one that just has not been separated out systematically yet. Although I have problems with this thinking, I agree with his approach of naming many of these new "species" after real-life seabird ecologists: I do miss common names such as Harcourt's Storm–Petrel, which actually was named for a real person for a reason, being replaced by the worthless and non-helpful (but allegedly descriptive) name Band-rumped Storm-Petrel (Huh? Aren't most of the dark storm-petrels band-rumped?).

The other problem that I have with his book involves the range maps. The first problem is that range maps should be presented for all of the species, even the rare ones. How else can we get an assessment of whether the species is expected to occur again? The second problem is that there are errors in several of the range maps for the Pacific species (I have no experience in the Atlantic). For example, Short-tailed Shearwaters also occur in both the US and Canadian Beaufort seas, where they have expanded their range eastward in the past 35 years. Another problem is with the range of Flesh-footed Shearwater in the central Gulf of Alaska; from my experience, this species is extremely rare there, so much so that the range map should indicate rarity in that offshore region; the same goes for Pink-footed Shearwater in that region. Finally, Buller's Shearwaters are indicated as being absent from the entire northwestern Pacific, whereas they occur east of Japan, in the confluence of the Oyashio and Kuroshio currents, fairly regularly. There are other examples, but these make the point.

These problems are minor, however, in comparison with the encyclopedic nature of the information that is presented here. This book truly lays out the learning of a master field ornithologist over the course of his lifetime, making one's job of learning these often-difficult birds a lot easier than anything that has been available previously. In my opinion, this book belongs on the bookshelves of seabird biologists, birders, and anyone else who wants to know just how good a field guide can be.—ROBERT H. DAY, ABR, Inc.—Environmental Research & Services, P. O. Box 80410, Fairbanks, AK, 99708-0410, USA

THE BIRD SPECIES/DIE VOGELARTEN. Systematics of the Bird Species and Subspecies of the World. Charadriiformes. By Norbert Bahr. Christ Media Natur, Minden, Germany. 2011. 191 pages. ISBN: 978-3-923757-11-4. $34.99.—This slender volume is the first of a series that will list all the species and subspecies of the birds of the world according to the latest classification, billed as a modern version of the 16 volume Peters Check-list published 1931–1987 by Harvard University Press. This volume, unnumbered, covers the order Charadriiformes. An introductory paragraph for the order and for each family summarizes the reasons for the classification accepted. There is a full citation (author, date, publication data, type locality) for each scientific name, with English and German names for each species. An extensive series of footnotes (262) gives subspecific synonyms or mentions alternate taxonomic or nomenclatural treatments. Statements of distribution are minimal, giving only the primary breeding and wintering ranges. All text (including footnotes) is in both English and German.

The development of techniques in molecular phylogenetics in the past couple of decades has led to significant changes in classification, and our understanding of relationships in this diverse order is greatly improved—or at least altered. The classification adopted for this volume relies heavily on the results of these studies, especially those by A. J. Baker and his colleagues. The order, consisting of 22 families, is divided into three suborders. Those who have not kept up on a paper-by-paper basis are likely to find some surprises, both in taxonomy and in the sequential listing of families and genera. Most regional and national check-lists will (probably) adopt most of these changes eventually. The AOU Check-list is one that is lagging in this respect. Among the important changes from historical listings accepted by Bahr but not (yet) by the AOU are recognition of the tundra plovers (genus *Pluvialis*) as a family distinct from other plovers, treatment of the skimmers (*Rynchops*) as a family distinct from terns, and the sequential listing of the alcids before, instead of after, the skuas, gulls and terns. *Larus smithsonianus* is separated from the Herring Gull, *L. argentatus*. There are other minor differences, as in the recognition of species and subspecies, but none that should cause a problem for any user. One may not agree with all the taxonomic decisions, but one will at least know their basis and can test the hypotheses.

Until there is a moratorium on research to allow lists to catch up (which should never happen), no list will be completely up to date. Bahr's book

was published before Gibson and Baker's study (Molecular Phylog. & Evol. 64:66–72, 2012) of calidridine (now arenariinine) sandpipers which suggested that five generally recognized genera should be collapsed into the single genus *Calidris* (see Banks, Zootaxa 3513:86–88, 2012). Strangely, Bahr went the opposite direction, recognizing 11 genera for this group of 24 species, resurrecting several long-unused names. This is surprising considering that earlier genetic studies have shown that genera in other sandpiper subfamilies (e.g., Tringinae), which Bahr followed, were previously over-split. To avoid the out-of-date problem, however, the series is complemented by a web site that will provide updates, adding taxa that were overlooked or that have been described since publication, <www.thebirdspecies.com>.

The introduction to this volume clearly outlines the author's concepts of the taxonomic categories used, and includes a clear statement that he follows the Comprehensive Biological Species Concept (Johnson et al., pp. 1470–1482, Proc. 22 IOC, 1999). Genera are based on molecular trees where available, or recent morphological studies, or traditional taxonomy. The superspecies rank is not used, but subspecies groups, often given species status by some authors, are marked. References are plentiful, documenting most taxonomic decisions. The comprehensive bibliography covers 20 pages; most references are less than 20 years old.

A useful appendix gives full citations for all scientific names mentioned in the footnotes. Another appendix is a list of authors of genera and species in the order; I fail to see the point of those three pages. There are separate indices of scientific, German, and English bird names.

This volume, and those that follow, will be a must for anyone who deals with subspecific taxonomy of the world's birds, particularly in collections. There are, of course, other lists of species and subspecies of birds of the world, published in one volume or in parts since the completion of the Peters series. Each has its virtues. This is the first, I believe, to be intended specifically as an authoritative successor to Peters. Whether it will serve that purpose will depend in part on the on the speed with which subsequent volumes are forthcoming. The publisher's notices in this volume indicate that the second will be out in 2012, but in fact it will not be available until late 2013. The number of volumes anticipated is not stated. As Witmer Stone said in 1932 in his review of volume 1 of Peters, we "welcome the appearance of [the] first volume and wish him all speed with the remaining nine" … which turned out to be 15.—RICHARD C. BANKS, 3201 Circle Hill Road, Alexandria, VA 22305, USA; e-mail: eudromia22@aol.com

THE BIRDS OF ALEXANDER WILSON-WILSON'S PHALAROPES (*PHALAROPUS TRICOLOR*)

In 1812 on his last trip through northern New York and New England, Wilson visited Charles Trowbridge's museum where he saw a single stuffed phalarope. He sketched the bird in a life-like pose and wrote a detailed description. Based on his examination he concluded that it was the Gray Phalarope (*Tringa lobata*) described by Turton and it is so labeled in the plate and text of the *American Ornithology*. However, Louis Jean Pierre Vieillot realized that it was a new species and in 1817 christened it *Phalaropus tricolor*, the scientific name that it retains to this day. Charles Lucien Bonaparte, wishing to honor Wilson's discovery and description of the new species, but recognizing the precedence of Vieillot's scientific name, gave the species its common name, Wilson's Phalarope.

Because Wilson saw only the single museum specimen, his portrayal of the species is ecologically inaccurate. In Wilson's later volumes he grouped species by habitat and painted them behaving as they were when he saw them. Since he had only a specimen on which to base his interpretation of the phalarope's habitat and behavior he grouped it with the Red Phalarope, identified from a putrid specimen he received in the mail, but then placed both phalaropes on a muddy shore near a Purple Gallinule with a Wilson's Plover running past. An American Coot swims in the shallow water.

Wilson completed the layout for the plate, but died before writing the species account. George Ord wrote the account based on Wilson's penciled notes, which Ord found very difficult to read.

Edward H. Burtt, Jr., Professor of Zoology,
Ohio Wesleyan University

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